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POPULATION BIOLOGY OF THE PACIFIC SARDINE (*SARDINOPS CAERULEA*)

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INTRODUCTION

The rise and fall of the fishery for Pacific sardines, *Sardinops caerulea* (Girard), is well known. The raw catch figures give a dramatic historical summary (fig. 1).

However, uncorrected and by themselves they do not provide an adequate picture of the population dynamics of the sardine. It is the aim of this study to:

1. Establish the relation between the annual catches and the corresponding population sizes, and from these, indirectly, estimate the sizes of the year classes;
2. Establish the relation between spawning stock size and year class size;
3. Examine the effect of the fishery on reproduction and, hence, on population size;
4. Consider the sardine population in relation to the food available to it in the environment and the effects of possible competitors; and
5. Attempt to determine the cause of the decline of the fishery, to indicate what might have been done in the past, and what could be done in the future, to reestablish the population.

The period covered by this study is 1932 to 1960, 29 years. This period was selected because the records prior to 1932 are inadequate for most analyses, and those subsequent to 1960 were not yet fully available. All of the basic data have been published and are readily available. For this reason, only the original data critical to the analyses at hand or required for orderly consideration of the arguments are reproduced.

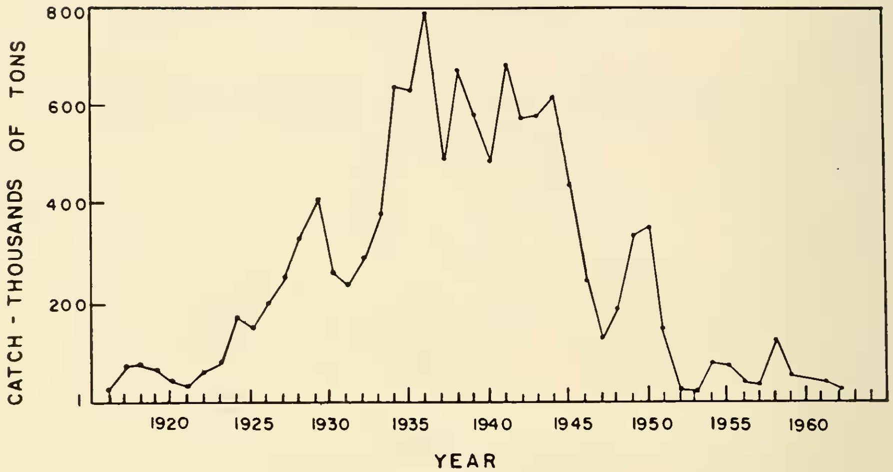

FIGURE 1. Seasonal catch in tons of sardines along the Pacific Coast. Each season includes June through the following May. Data from California Cooperative Oceanic Fisheries Investigations Reports, vols. VIII and X.

HISTORY OF THE FISHERY

The history of the sardine fishery to 1942 has been considered in detail by Schaefer, Sette, and Marr (1951). Very briefly, catches were trivial (300 to 2,000 tons per year) in the early years, and a sustained fishery and canning industry did not develop until stimulated by the demand for food during World War I. Starting in 1915, the catch increased continually, with only minor setbacks, until the maximum catch of nearly 800,000 tons was landed in the 1936–1937 season. (A season roughly covers the period from late summer to early spring. Henceforth, each season will be identified by the year in which it started.) Thereafter, catches declined progressively, with relatively short-lived reversals, until, in the 1960's, the landings were of the order of only 20,000 tons annually.

Fishing effort in California, the principal producer, increased steadily through the period of rising catches, reaching 1,237 boat months in 1936. Effort remained approximately at this level (921–1,526 boat months) through 1950 (Clark and Daugherty, 1952). After 1950, the effort declined as vessels left the sardine fleet through bankruptcy or diversion to other fisheries (Clark, 1956). Through 1936 the increased landings were largely a result of increased fishing stimulated by economic demand (Schaefer, Sette, and Marr, 1951). The major features of the subsequent decline cannot, however, be attributed to economic factors, for information in trade publications and related private and government reports shows that during and subsequent to World War II

the demand has always exceeded the supply. Thus, a major decline in the population is clearly implicated in the decline in landings.

Examination of the catches by region (table 1) reveals several interesting major features: The fishery began first in California. Later (1925), large catches were made in the Pacific Northwest. These increased with the California landings but always remained a small part of the total (10 to 20 per cent). Judging by the results of tagging experiments (Janssen, 1948), the Pacific Northwest landings were probably mostly based on segments of the population participating in an annual northerly migration. The northern fishery disappeared completely after 1948. This was followed by a progressive southward shift of the site of most landings. In 1963, the fishery was centered off Baja California, and field reports indicate that current landings are mostly from the southern half of Baja California. Thus, the decline of the sardine has been characterized by a progressive decrease in range as well as numbers.

One other useful point can be derived from the crude statistics. Beginning in 1934 and ending in 1945, landings fluctuated between 4 and 6×10^5 tons (table 1) although fishing effort during 1934 and 1935 was only about 67 per cent of that expended during the balance of this period of high, relatively stable catches. This reduction in catch per unit of effort may represent the "fishing down" of a stock, with landings subsequent to 1935 more nearly dependent on annual production.

SCIENTIFIC INVESTIGATIONS OF SARDINES

Species of the genus *Sardinops* are found everywhere in temperate and subtropical waters along coasts. They are the object of fisheries wherever they occur, and are, or were, the basis of major fisheries in Japan, the Pacific Coast of the United States, and South Africa. Except for the last, all of these fisheries have experienced disconcerting fluctuations in yield. This, together with the importance of the fisheries, has led to a great deal of research and publication. Wheeler's (1931) worldwide bibliography of sardines lists over 1,500 references. Many of the papers cited concern "sardine-like" fishes. Japanese references, however, are not included, the omission perhaps balancing the commission. A more modern review source on sardine research is the Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species (Rosa and Murphy, 1960). This three-volume set contains concise synopses of the biology of sardine populations on a worldwide basis, as well as research and review papers.

The Pacific sardine has been the subject of extensive research as attested to by the inclusion of 158 references to the species in "An annotated bibliography of research in economically important species of California fish and game" (Scheuermann, 1958), and its two supplements (Calif. Dept. of Fish

TABLE 1. *Seasonal catch in tons of sardines along the Pacific Coast; each season includes June through the following May.**

	Pacific Northwest				California							
					Northern California							
Season	British Columbia	Wash-ington	Oregon	Total	Reduction Ships	San Francisco	Monterey	Total	Southern California	Total California	Baja California	Grand Total
1916–17	–	–	–	–	–	–	7,710	7,710	19,820	27,530	–	27,530
1917–18	80	–	–	80	–	70	23,810	23,880	48,700	72,580	–	72,660
1918–19	3,640	–	–	3,640	–	450	35,750	36,200	39,340	75,540	–	79,180
1919–20	3,280	–	–	3,280	–	1,000	43,040	44,040	22,990	67,030	–	70,310
1920–21	4,400	–	–	4,400	–	230	24,960	25,190	13,260	38,450	–	42,850
1921–22	990	–	–	990	–	80	16,290	16,370	20,130	36,500	–	37,490
1922–23	1,020	–	–	1,020	–	110	29,210	29,320	35,790	65,110	–	66,130
1923–24	970	–	–	970	–	190	45,920	46,110	37,820	83,930	–	84,900
1924–25	1,370	–	–	1,370	–	560	67,310	67,870	105,150	173,020	–	174,390
1925–26	15,950	–	–	15,950	–	560	69,010	69,570	67,700	137,270	–	153,220
1926–27	48,500	–	–	48,500	–	3,520	81,860	85,380	66,830	152,210	–	200,710
1927–28	68,430	–	–	68,430	–	16,690	98,020	114,710	72,550	187,260	–	255,690
1928–29	80,510	–	–	80,510	–	13,520	120,290	133,810	120,670	254,480	–	334,990
1929–30	86,340	–	–	86,340	–	21,960	160,050	182,010	143,160	325,170	–	411,510
1930–31	75,070	–	–	75,070	10,960	25,970	109,620	146,550	38,570	185,120	–	260,190
1931–32	73,600	–	–	73,600	31,040	21,607	69,078	121,725	42,920	164,645	–	238,245
1932–33	44,350	–	–	44,350	58,790	18,634	89,599	167,023	83,667	250,690	–	295,040
1933–34	4,050	–	–	4,050	67,820	36,336	152,480	256,636	126,793	383,429	–	387,479
1934–35	43,000	–	–	43,000	112,040	68,477	230,854	411,371	183,683	595,054	–	638,054
1935–36	45,320	10	26,230	71,560	150,830	76,147	184,470	411,447	149,051	560,498	–	632,058
1936–37	44,450	6,560	14,200	65,210	235,610	141,099	206,706	583,415	142,709	726,124	–	791,334
1937–38	48,080	17,100	16,660	81,840	67,580	133,718	104,936	306,234	110,330	416,564	–	498,404
1938–39	51,770	26,480	17,020	95,270	43,890	201,200	180,994	426,084	149,203	575,287	–	670,557
1939–40	5,520	17,760	22,330	45,610	–	212,453	227,874	440,327	96,939	537,266	–	582,876

Table 1. *Continued.*

	Pacific Northwest				California							
						Northern California						
Season	British Columbia	Wash-ington	Oregon	Total	Reduction Ships	San Francisco	Monterey	Total	Southern California	Total California	Baja California	Grand Total
1940–41	28,770	810	3,160	32,740	–	118,092	165,698	283,790	176,794	460,584	–	493,324
1941–42	60,050	17,100	15,850	93,000	–	186,589	250,287	436,876	150,497	587,373	–	680,373
1942–43	65,880	580	1,950	68,410	–	115,884	184,399	300,283	204,378	504,661	–	573,071
1943–44	88,740	10,440	1,820	101,000	–	126,512	213,616	340,128	138,001	478,129	–	579,129
1944–45	59,120	20	–	59,140	–	136,598	237,246	373,844	181,061	554,905	–	614,045
1945–46	34,300	2,310	90	36,700	–	84,103	145,519	229,622	174,061	403,683	–	440,383
1946–47	3,990	6,140	3,960	14,090	–	2,869	31,391	34,260	199,542	233,802	–	247,892
1947–48	490	1,360	6,930	8,780	–	94	17,630	17,724	103,617	121,341	–	130,121
1948–49	–	50	5,320	5,370	–	112	47,862	47,974	135,752	183,726	–	189,096
1949–50	–	–	–	–	–	17,442	131,769	149,211	189,714	338,925	–	338,925
1950–51	–	–	–	–	–	12,727	33,699	46,426	306,662	353,088	–	353,088
1951–52	–	–	–	–	–	82	15,897	15,979	113,125	129,104	16,184	145,288
1952–53	–	–	–	–	–	–	49	49	5,662	5,711	9,162	14,873
1953–54	–	–	–	–	–	–	58	58	4,434	4,492	14,306	18,798
1954–55	–	–	–	–	–	–	856	856	67,609	68,465	12,440	80,905
1955–56	–	–	–	–	–	–	518	518	73,943	74,461	4,207	78,668
1956–57	–	–	–	–	–	–	63	63	33,580	33,643	13,655	47,298
1957–58	–	–	–	–	–	–	17	17	22,255	22,272	9,924	32,196
1958–59	–	–	–	–	–	–	24,701	24,701	79,270	103,971	22,334	126,305
1959–60	–	–	–	–	–	–	16,109	16,109	21,146	37,255	21,424	58,679
1960–61	–	–	–	–	–	–	–	2,340	26,538	28,878	19,899	48,777
1961–62	–	–	–	–	–	–	–	2,231	23,297	25,526	21,270	46,798
1962–63	–	–	–	–	–	–	–	1,211	2,961	4,172	14,620	18,793

* Data from California Cooperative Oceanic Fisheries Investigations Reports, vols. VIII and X.

and Game 1961, 1962). Especially useful among these papers are two major reviews concerning the Pacific sardine population problem, Clark and Marr (1955) and Marr (1960), and also a succinct synopsis of the biology, ecology, and fishery for the Pacific sardine (Ahlstrom, 1960).

Research on the Pacific sardine may be briefly, if somewhat inadequately, characterized as follows: From 1920 to 1938, effort was concentrated on describing the fishery, the migration of the sardine, and its biology, *i.e.,* growth, fecundity, etc. Beginning in 1949, active research interest expanded to include studies of spawning and the environment as a determinant in spawning and fishing success, as well as attempts to understand the population dynamics of the sardine. This trend was accelerated in 1949 with the formation of the Marine Research Committee of the State of California and the establishment of the California Cooperative Oceanic Fishery Investigations. (See California Cooperative Oceanic Fishery Investigations Reports, vols. 1–9.)

Some generalizations pertinent to the population problem can be drawn from the accumulated literature. In all sardine populations that have been studied, there is clear evidence of large fluctuations in year class size. These seem unrelated to spawning stock size and, therefore, are almost certainly a function of the environment. In all instances, there are also considerable variations from year to year in the catchability of the population. These variations are related to the behavioral and distributional responses of the population to differences in environment. This is a problem even in benthic fisheries, but is particularly severe in pelagic fisheries. Some, tuna, for example, overcome the environmentally induced vagaries by shifting the fleet with the fish. The sardine fisheries, however, are mostly day fisheries so that if the population shifts away from the fishing ports it becomes unavailable to the fleets.

The fluctuation in the catchability of the population means that average catch per unit of effort is not a precise measure of population size. This imprecision, combined with the variations of year class size independent of spawning stock size, has made it difficult to determine analytically the effect of the fishery on stock size, and, in turn, the relation between stock size and reproductive success.

METHOD OF ESTIMATING POPULATION SIZE

The Catch Equation

Providing the individuals in the catch can be aged, the most efficient way of estimating population size from catches is to solve for the population in numbers and later convert to biomass. The basic concepts and equations are well known (*e.g.,* Ricker, 1958a; Beverton and Holt, 1956; Widrig, 1954) and are considered here in summary form only, following Beverton and Holt, 1957.

For simplicity, consider only a single year class (cohort or age class) subject to natural mortality and fishing mortality. If it is assumed that the rate of change in numbers is proportional to the population size and that the proportionality constant is the coefficient of natural mortality (M) plus the coefficient of fishing mortality (F), the expression for population size at time t is:

$$N_t = N_0 e^{-(F+M)(t-t_0)} \tag{1}$$

where N_0 is the number present at time t_0. For the sake of simplicity, $t - t_0$ will henceforth be assumed to have a value of 1 (one year), yielding:

$$N_t = N_0 e^{-(F+M)}. \tag{2}$$

The fishing mortality coefficient (F) may be considered as the product of the instantaneous effect of one unit of fishing effort (q) and the number of units of fishing effort (f). In these terms, the fraction surviving during the interval is:

$$\frac{N_t}{N_0} = e^{-(qf+M)}, \tag{3}$$

and $1 - e^{-(qf+M)}$ is the fraction that dies. The catch (C) may then be expressed as:

$$C_i = N_i \frac{qf_i}{qf_i + M}(1 - e^{-qf_i - M}), \tag{4}$$

or alternately:

$$C_i = N_i \frac{F_i}{F_i + M}(1 - e^{-F_i - M}), \tag{5}$$

where $qf_i/(qf_i + M)$ is the fraction of the total deaths ascribable to the fishery. (The subscript i refers to the beginning of a time period when applied to N and the entire time period in all other instances. M is regarded as a constant.) From this basic equation, it can be shown (Ricker, 1958a, p. 27) that the average catch per unit of effort, C/f, is proportional to average abundance during the fishing season ($\overline{N}$), if natural mortality and fishing mortality are both applied at a constant rate through the time period in question, *e.g.*, a year. It has been shown that lack of constancy is not a serious source of bias in the usual situation of a fishery extending over a significant portion of the year (Ricker, 1958a).

Previous Solutions of the Catch Equation (4)

Equation (4) contains three unknowns, N_i, q, and M, and only two

knowns, C_i and f_i. It can only be solved if two more pieces of information are obtained. In theory, this extra information can be obtained by using equation (3) in logarithmic form:

$$\ln \frac{N_i}{N_{i+1}} = qf_i + M = Z_i, \tag{6}$$

and estimating $\ln N_i/(N_{i+1})$ by $\ln (C_i/f_i \div C_{i+1}/f_{i+1})$. If q and M are assumed constant and fishing effort is known, a linear regression of Z on f will supply the extra information as the slope of the regression can be equated to q, and the value of Z when $f = 0$ is an estimate of M. One problem with this solution is that unless (f) is the same for each year in an adjacent pair, bias is introduced. Usable methods for overcoming this problem, based on an assumed constancy of q, have been elaborated by Beverton and Holt (1957), and Paloheimo (1961). Apart from the usual sampling problems, the principal difficulty with their methods resides in the assumption that (q) the coefficient expressing the effect of one unit of fishing effort remains essentially constant from year to year. If it does not, (f) is not measured even if exact knowledge of the total effort is at hand. This means that both f and Z will be subject to error and the errors will be correlated because Z is estimated by an expression involving f. As pointed out by Paloheimo (1961), efficient techniques of fitting a straight line when errors in the ordinate and abscissa are not independent but correlated are not known. In the instance of the catch statistics of the Pacific sardine, these errors are sufficiently large to result in estimates of natural mortality that are large and negative. (See, for example, Widrig, 1954.)

Schaefer (1954) applied a quite different approach, originally developed for the analysis of tuna landing statistics. His method circumvents solving the catch equation directly in that the observed annual catch per unit of effort is employed as a measure of population size. As already mentioned, such measures are very imprecise in the instance of the sardine because of wide year-to-year variation in the catchability of the population. This problem could be minimized, even in the sardine fishery, if data for sufficient years were available to permit reliable estimation of an average catch per unit of effort at each stock size.

Another approach to estimating the relative size of the sardine population has been to use the concept of "virtual population" first employed by Fry (1949). The method is simple if aged catches are available. The relative population size during a given year is estimated as the catches of all the age-classes present in the population that year summed over as many years as they appear in the fishery. This can also be used to estimate relative year class strength and, if the age-classes accumulated are mature fish, relative spawning stock. For this method to provide estimates of the total population

size, natural mortality must be zero; for estimates of relative population size, the fishing mortality rate and natural mortality rate must be constant over the entire series of years under consideration. Neither of these requirements is entirely satisfied by any fishery, particularly not by the sardine fishery in which fishing effort has varied fourfold and catchability has varied even more.

The problems associated with the virtual population have been recognized for some time and were dealt with analytically by Paloheimo (1958), and, especially, by Bishop (1959). Uncorrected virtual populations were used by Clark and Marr (1955), by Marr (1960), Radovich (1962), and MacGregor (1964). As an example of the misleading results this method can yield, Radovich (1962) estimated the spawning stock during 1932 as about the same size as in 1943. The fishing effort during the early thirties was about half that in the early forties, so the 1932 spawning stock might have been much larger than the 1943 stock (on the face of it by as much as 2 times). Similar problems of the same magnitude apply to his estimates of year class size.

Though methods have been developed for quantitatively correcting population estimates based on virtual populations, these cannot be applied to the Pacific sardine statistics because they all depend on estimating relative fishing mortality solely on the basis of the measurement of year-to-year changes in fishing effort. Changes in availability (or catchability) from year to year are not included.

The difficulty common to all these methods of solving the catch equation (4), even inferentially, for the Pacific sardine is that because of changing catchability, it is not realistic to assume that a unit of fishing effort has the same impact on the population from one year to the next. (This is amply documented in table 11, p. 38, where apparent survival rates greater than 1.0 are obtained from the catch per unit of effort statistics.) The same problem in another form also applies to the more stable situation represented by demersal fisheries. In that situation, the population is frequently more vulnerable on one ground than another, and if the proportion of the fishing in each subarea varies from year to year, effort alone will not be linearly related to the fishing mortality coefficient.

Beverton and Holt (1957) have developed a method for computing a derived measure, *i.e.*, effective fishing effort, from what amounts to changes in catchability induced by the behavior of the fishing fleet. Although this method overcomes difficulties that undoubtedly exist in the sardine data, it provides no basis for solving for changes in catchability due to changes in the behavior and distribution of the sardine, which appear to be of great magnitude. Widrig (1954) fully recognized the importance of the problem and developed one approach. The approach used in this study is easier to evaluate. It is considered in detail in Murphy, 1965, and in summary form below.

Solving the Catch Equation

Consider first the catches of a cohort of fish during two successive seasons. Only the year classes that are fully recruited into the fishery will be included. The catch during one season is represented by equation (5). The catch in the following season is represented by equation (7):

$$C_{i+1} = N_i e^{-M-F_i} \frac{F_{i+1}}{F_{i+1}+M}(1-e^{-F_{i+1}-M}), \tag{7}$$

where $N_i e^{-M-F_i}$ is the number of individuals of the cohort surviving at the start of year $i+1$. The ratio of catches is then:

$$\frac{C_{i+1}}{C_i} = e^{-M-F_i} \frac{F_{i+1}}{F_{i+1}+M} \; \frac{F_{i+M}}{F_i} \; \frac{(1-e^{-F_{i+1}-M})}{(1-e^{-F_i-M})}. \tag{8}$$

Homologous equations can be written for all pairs of successive catches. The series expanded to j years (*i.e.*, the total years for which catch data is available) yields $j-1$ equations similar to (8), containing $j+1$ unknowns. Such a system of equations can be solved explicitly yielding j solutions of F, provided that two additional independent pieces of information are made available. These might be an estimate of the natural mortality coefficient (M) and an independent estimate of F for any year in the series. The latter might be derived from tagging experiments or survey-removal estimates (Chapman and Murphy, in press). Fortunately for many of the major fisheries of the world, *e.g.*, the Pacific halibut or the Antarctic fin whales, such auxiliary information is available, at least in approximate form.

General Solution

A system of equations of the type of (8) can only be solved by iteration. The approach can be shown more easily when the terms have been collected as follows:

$$Z_i = F_i + M \qquad\qquad p^* = \frac{C_{i+1}}{C_i}$$

$$S_i = e^{-M-F_i} = \frac{N_{i+1}}{N_i}.$$

Substituting and rearranging, equation (8) becomes (9):

$$p^*_i = S_i \frac{F_{i+1}}{F_i}\left[\frac{Z_i}{1-S_i}\right]\left[\frac{1-S_{i+1}}{Z_{i+1}}\right]. \tag{9}$$

If we assume that M and F_i are known, equation (9) can be rearranged to (10) and solved by iteration.

$$F_{i+1} = \frac{p^*_i}{S_i} F_i \left[\frac{1-S_i}{Z_i}\right]\left[\frac{Z_{i+1}}{1-S_{i+1}}\right]. \tag{10}$$

Once a value for F_{i+1} has been obtained, F_{i+2} may be solved for, and so forth, until a value for F_j (the last year of catch information) is obtained. Back calculation from midseries (say from F_{i+10}) which is also possible, is more laborious as an additional nonlinear term (S_i) is involved. An alternate method if the year with the known F is partway down the series is to start with a trial value of F_i, compute down to the known F, and, depending on the result, adjust the trial value of F_i until satisfactory agreement with the known F is achieved. A computer is essential for either computational scheme because the solution of each successive equation is dependent on the accuracy of the preceding solution. Achieving the required accuracy by hand computation would simply be too time-consuming.

Once the system of equations has been solved yielding the series of j solutions of F, the component parts of F can be examined. For example, if effort has been measured, F may be considered a product of fishing effort (f) and the coefficient of fishing power (q), which are now all variables. Variation in (q) may be examined as a function of the behavior of the fish, the weather, or as an indication of changes in the efficiency of the fleet. Under some circumstances, it may be more useful to divide F initially into its components. This approach will be considered next.

SOLUTION BY PREPARTITIONING F

If measurements of fishing effort are available, it may be desirable to begin by prepartitioning F into its components. As already stated, the genesis of this solution was a reexamination of Widrig's 1954 results. He approached the problem by assuming a population model as follows: During a given fishing season the fishable stock was divided into two components, one fully available to the fishery and a second not available at all; between fishing seasons there was complete mixing. This concept is expressed in equation (11) which is a modification of Widrig's (2):

$$(11) \qquad \frac{N_{i+1}}{N_i} = e^{-F_i - M} = r_i e^{-M - vf_i} + (1 - r_i) e^{-M},$$

where r is the fraction of the population available to the fishery and v is a constant modifying f.

As this model proved to be difficult to manipulate, a simpler model incorporating the idea of variation in availability was examined:

$$(12) \qquad \frac{N_{i+1}}{N_i} = e^{-M - (rvf)_i} = S_i,$$

where v is a residual constant and r is a variable modifying vf and reflecting changes in the effectiveness of the gear due to weather, behavior, and distribution of fish, and/or errors in measuring f. Therefore, rv is a variable catchability coefficient equal to the constant q used earlier. The conceptual

difference between equations (11) and (12) is primarily that equation (12) requires that all of the population be equally available to the fishery during a given season, *i.e.*, the mixing process is continuous within and between seasons, but that, as in Widrig's model, the average availability (r) varies among seasons. Widrig's model (11) might be more appropriate if the fishing season is very short and equation (12) if the fishing season is long.

Whatever the philosophical difference, there is little difference in the numerical results, for rearranging, taking logarithms, and approximations, equation (11) becomes exponential and logarithmic by the first terms in the appropriate series:

$$\begin{aligned} Z &= M - \ln\left[re^{-vf} + (1-r)\right] \\ &\sim M - \ln\left[r(1-vf) + (1-r)\right] \\ &\sim M - (-rvf) \\ \therefore Z &\sim M + rvf\,. \end{aligned}$$

This is equation (12) in logarithmic form. Evaluation of (11) and (12) using values appropriate to a fairly heavy fishery confirms the near equality.

Equation (4) can be rewritten as follows:

$$C_i = N_i \frac{r_i v f_i}{r_i v f_i + M}\left(1 - e^{-r_i v f_i - M}\right), \tag{13}$$

where the symbols have the meanings designated for equation (12).

Given a series of j years of data, a series of equations analogous to those developed previously (9, 10) can be obtained:

$$\frac{C_{i+1}/f_{i+1}}{C_i/f_1} = S^* = S_i \frac{vr_{i+1}}{vr_i}\left[\frac{1-S_{i+1}}{Z_{i+1}}\right]\left[\frac{Z_i}{1-S_i}\right]. \tag{14}$$

S^* in (14) is the catch per unit of effort in year $i+1$ divided by the catch per unit of effort in year i, whereas p^* in (9) is simply the quotient of the catches. For purposes of evaluation, equation (14) can be simplified and rearranged in the form of (15):

$$r_{i+1} = \frac{S^*_i}{S_i} r_i \left[\frac{Z_{i+1}}{1-S_{i+1}}\right]\left[\frac{1-S_i}{Z_i}\right], \tag{15}$$

with the pattern of solution essentially similar to that of (10). The algebraic identity of the two methods may be appreciated by comparing equations (10) and (15). If when using this second method one has a series in which effort has not been measured, and one simply inserts the same arbitrary large number for each f, the two methods converge in that they are both free of the necessity of measuring f in order to evaluate F.

Estimating Younger Age-classes

The calculations already described deal only with the older classes or

cohorts which are presumed to share the same values of M and F. Once the value of F is computed for a given year, the population N of each of these age-classes at the beginning of the fishing season may be solved for in equation (5). Often, however, it is desirable to estimate the population size of younger cohorts or age-groups that are not fully recruited. These population sizes might serve, for example, as estimates of year class size.

From equations similar to (5) and (2), the following can be derived:

$$C_0 = N_1 \frac{F_0}{F_0 + M}(e^{F_0+M} - 1), \tag{16}$$

where

C_0 = Catch of the year class not fully recruited, *i.e.*, not fully vulnerable to the fishery.

F_0 = Fishing rate of the year class not fully recruited.

N_1 = Size of the year class one year later when it is fully recruited (this will have already been estimated).

The value of F_0 can be estimated by iteration and from this N_0, the size of the younger cohort, can be obtained through equation (17):

$$N_1 = N_0 e^{-F_0-M} \tag{17}$$

This procedure can be extended successively to younger cohorts so long as the catch of these is substantial enough to provide the basis for an estimate.

APPLICATION TO THE PACIFIC SARDINE

Background Information and Extra Degrees of Freedom

The information required for solution of the series of sardine catch data falls into two major categories. The record of aged catches, with or without attendant information on fishing effort, is the primary source of information. The secondary information from which the additional degrees of freedom are drawn may be divided into two categories: independently derived estimates of rates, *i.e.*, natural mortality and fishing rates, and independent estimates of population size.

Mortality Rates

Natural mortality. Obtaining realistic estimates of natural mortality has proven to be an intractable problem in most fish population studies. The difficulties are discussed at length by Beverton and Holt (1957), and Paloheimo (1958 and 1961). As already pointed out, natural mortality can, in theory, be estimated from the regression of total mortality on effort (equation 6). As shown by Widrig (1954), however, this gives a negative value for the natural mortality coefficient (M) for the sardine. This un-

realistic result is not substantially improved by applying Paloheimo's method (1961). The problem is not unique to the sardine series. Beverton and Holt (1957), in their analysis of the plaice population of the North Sea, surely the most intensively studied fish population in the world, were able to derive their working estimate of M only because of the availability of records of the population from immediately after World War II when fishing mortality was nearly zero.

Silliman (1943) devised a simple method which overcomes many of these theoretical and practical problems. It requires two periods in the fishery when fishing effort is relatively stable at different levels. An additional requirement is that the periods be long enough so that the effect of uneven recruitment and/or availability is averaged out of the two catch curves from which estimates of survival (S) are derived. His method can be succinctly expressed by modifying equation 14.89 in Beverton and Holt (1957) as follows:

$$M = \frac{Z_1 f_2 - Z_2 f_1}{f_2 - f_1}, \tag{18}$$

where

M = Coefficient of natural mortality.
Z = Instantaneous total mortality coefficient ($Z = -\ln S$).
f = Total fishing effort, or relative measure of total fishing effort.
1, 2 = Subscripts referring to the two time periods.

Using Silliman's values of Z for the two periods, solution of the equation yields a value of M of 0.153. Clark and Marr (1955) suggested that the value was too low. They attributed this to Silliman's reliance upon the catch curve from a single season's fishing (1941–1942) as an estimate of survival during period two (1937–1942). Additional data strongly suggest that increased recruitment during this period resulted in too low an apparent survival based on the single year (1941–1942). Ricker (1958a) suggested a progressive, undetected increase in the efficiency of the gear as a possible cause.

In view of the uncertainty about Silliman's estimate of M, the values of f and Z have been reestimated and used to calculate a new value of M. In this, the early period 1925–1932 used by Silliman was retained, but more years (1937–1945) were used for the later period.

Total California effort figures for the period 1937–1945 were taken from Clark and Daugherty (1952). It ranged from 1,008 boat months in 1942 to 1,401 boat months in 1938, with a mean of 1,251 for the 9-year period.

Effort for the early period must be estimated. Silliman (1943) stated

that it was about one-fourth of the effort during the period 1937–1941, but did not supply details, partly because studies on effort were incomplete. Though a continuous series of values of fishing effort is available subsequent to 1932, none is available prior to that time. Fortunately, the year 1932 is near the end of the period when, as stated by Clark and Daugherty, ". . . the daily tonnage delivered by fishing boats was determined by processing plants and not by the availability of sardines on the fishing grounds." This suggests that catch may have been proportional to effort prior to 1932, and that the earlier effort can be estimated by simply extrapolating backwards using the 1932 ratio of tons to effort as the base point. The resultant average effort is 369 boat months for the period 1925 to 1932. Preliminary analysis by the methods developed in this study indicated that the effort in 1932 was only half as effective as the average for 1937–1945, *i.e.,* (q) was only half as large. This could be the result of low availability during 1932, or due to the failure of the estimation method developed by Clark (1939) to compensate for technological improvements in the fishery, or, more likely, some combination of the two. Therefore, a more realistic estimate of average effort for the period 1925–1932 is 185 boat months.

Total mortalities for the two periods were estimated as follows. For the earlier period, age data from the catches were not available, but size frequencies were (Clark, 1936). Silliman (1943), using the methods he later described (1945), deduced the age composition from the length composition, and from this computed an average annual survival (S) of 0.60 for the period 1925–1932 ($Z = 0.5108$) in the California fishery.

For the later period (1937–1945), age composition data are available for the California catches (Wolf, 1961). The pertinent data are given in table 2. They were derived from Wolf's summary, which includes only catches from which the fish were aged, by adjusting them upwards for the tonnage not aged. Only those year classes that are represented in the catches during each of the 9 years are used and only the well-represented, fully recruited, ages are employed (three to six). The estimate of survival (S) derived by summing ages three to five and dividing by the sum of ages four to six is 0.3595 and Z is 1.0230. These same data are plotted logarithmically in figure 2. The near fit to a straight line suggests that the condition of essentially constant total mortality for the years under consideration is met. The algebraic solution is preferred to a calculation based on the slope of the line because it weights all data equally.

Using $Z = 1.0230$ for the later period, Silliman's estimate of $Z = 0.5108$ for the earlier period, and the several estimates of the relative amount of effort between the two periods developed above, equation (18) yields the results in table 3. While the lowest estimate of M is doubtless much too low, since there is good evidence that the crude figures overestimate the

Table 2. *Age composition of the California catch of Pacific sardines 1937–1945.*

Fishing Year	Numbers in Millions at Age				
	3	4	5	6	7
1937	541	614	403	106	73
1938	885	185	213	126	27
1939	1,234	281	59	76	24
1940	1,082	298	48	22	9
1941	1,562	282	69	11	5
1942	1,734	711	161	52	9
1943	971	1,025	321	83	23
1944	752	586	555	192	71
1945	848	485	200	95	42

1932 effort, the highest estimate is probably high, as some of the lack of effectiveness of the 1932 effort was probably due to the unavailability of the population, a condition that almost certainly did not apply throughout the entire 1925–1932 period.

Therefore, although some arbitrariness is involved, a value of M of 0.40 has been selected as reasonable. It probably fulfills the basic analytical need that M must be estimated with sufficient precision so that year-to-year errors are small relative to the magnitude of the fishing mortality coefficient.

Fishing mortality. Estimates of average fishing mortality for the two periods (table 3) were obtained from the relationship $Z = F + M$. Other estimates have been derived from certain survey data and from tagging experiments.

The use of survey-removal data to estimate fishing and natural mortality rates has been examined in detail by Chapman and Murphy (1965). Only those aspects pertinent to this study are considered here. The method stems from equation (5) and requires that the harvest of a population of animals be classifiable into two groups, one of which is more vulnerable than the other to harvest, and surveys that measure the two groups in proportion to their true abundances before and after the harvest period. It must also be assumed that the natural mortality of the two classifications is the same.

The survey-removal method involves solution of two simultaneous equations of the form of (5). If natural mortality is assumed constant (as specified above) and the catches of the two classes are known, there will be five unknowns in two equations. Two of the three needed extra pieces of information are supplied by the ratios of the abundance of the two classes before and after the harvest. If an estimate of natural mortality (M) is available, it will supply the fifth degree of freedom, but it has been shown (Chapman and Murphy, 1965) that the estimates of the values of fishing mortality (F) and of the population at the time of the survey (N) are so nearly in-

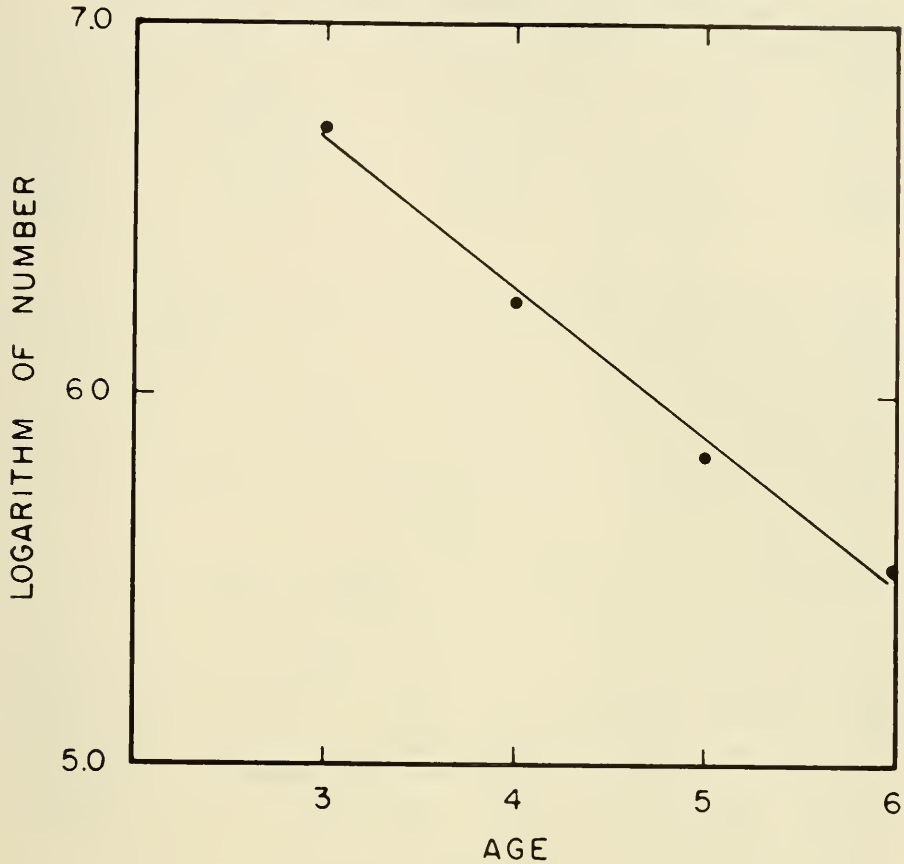

FIGURE 2. Logarithms of numbers of sardines as a function of age, California Catch, 1934–1938 year classes inclusive. Data from table 2.

dependent of M that even a reasonable guess of M will provide close working estimates of the desired quantities.

The possibility of classifying sardines into two groups is clearly shown in figure 3, a catch curve based on the average catch per boat month 1932–1954. While the catches of two-year-olds were substantial, their vulnerability to fishing was about 50 per cent smaller than that of the three-year and older fish. Otherwise, one would expect a relative catch of approximately the number shown by extrapolation of the straight right-hand limb of the curve. The straight line indicates that total mortality is constant from age three. Therefore, either both fishing and natural mortailty are constant between ages or they are both changing in an exactly compensatory way which seems unlikely.

TABLE 3. *Computation of* M *and* F *for the years 1925–1932 and 1937–1945, using the Silliman method.*

Ratio of Fishing Effort	Natural Mortality (M)	Fishing Mortality (F)	
		1925–1932	1937–1945
369 : 1,251	0.2965	0.2143	0.7265
1 : 4.00 (from Silliman)	0.3400	0.1708	0.6830
185 : 1,251	0.4222	0.0886	0.6008

Survey data before and after the 1950 fishing season were reported by Radovich (1952). Sardines were located at night by surface sighting, echo sounding, or by attracting fish with a 750-watt light. They were then sampled by dynamiting and recovering up to 100 of the immobilized fish. There is every reason to expect that the survey technique overcomes the bias of the commercial fishery with respect to the younger, smaller age-classes, and, lacking information to the contrary, I am assuming that they sampled the various age-classes in proportion to their abundance.

The results are reported on the basis of aged catches per standard night of scouting in seven zones along the coast between Pt. Delaga in California (39° 60′ N.) and Cabo San Lazaro in Baja California (25° 00′ N.) (Radovich, 1952, tables 2 and 4). In order to make these results representative of the total population, some sort of areal weighting is required. In the absence of precise information on the distribution of the population, weighting was done on the basis of shoreline because it lends slightly greater weight to the area where the Southern California eddy, roughly Pt. Conception to San Diego (Reid, Roden, and Wyllie, 1958), and the presence of offshore islands may increase the offshore extent of the habitat of the sardine.

In order to reduce the effect of minor variations of the shoreline, weighting factors were obtained with a map measure from a $1:5.4 \times 10^6$ scale map. Islands were not included. The results of applying these factors to the values in Radovich's published summaries are shown in table 4. The additional data in table 4 are the age compostion of the commerical catch during the intervening year and the computed apparent survival rates and coefficients of total mortality by year class. The latter determinations, of course, involve the assumption that the "efficiency" of the 1951 survey was the same as in 1950, as well as the assumption that the year classes were sampled proportionately within surveys. Only the second assumption is necessary for solution of the equations estimating fishing rate by the method of Chapman and Murphy (1965).

Of the several year classes in table 4, the 1948 class, which was 2 years old during the 1950 fishing season, is used as the less than fully available group. For the fully available group, either all older ages or only the 1947 year class could be used. The latter was selected because use of only

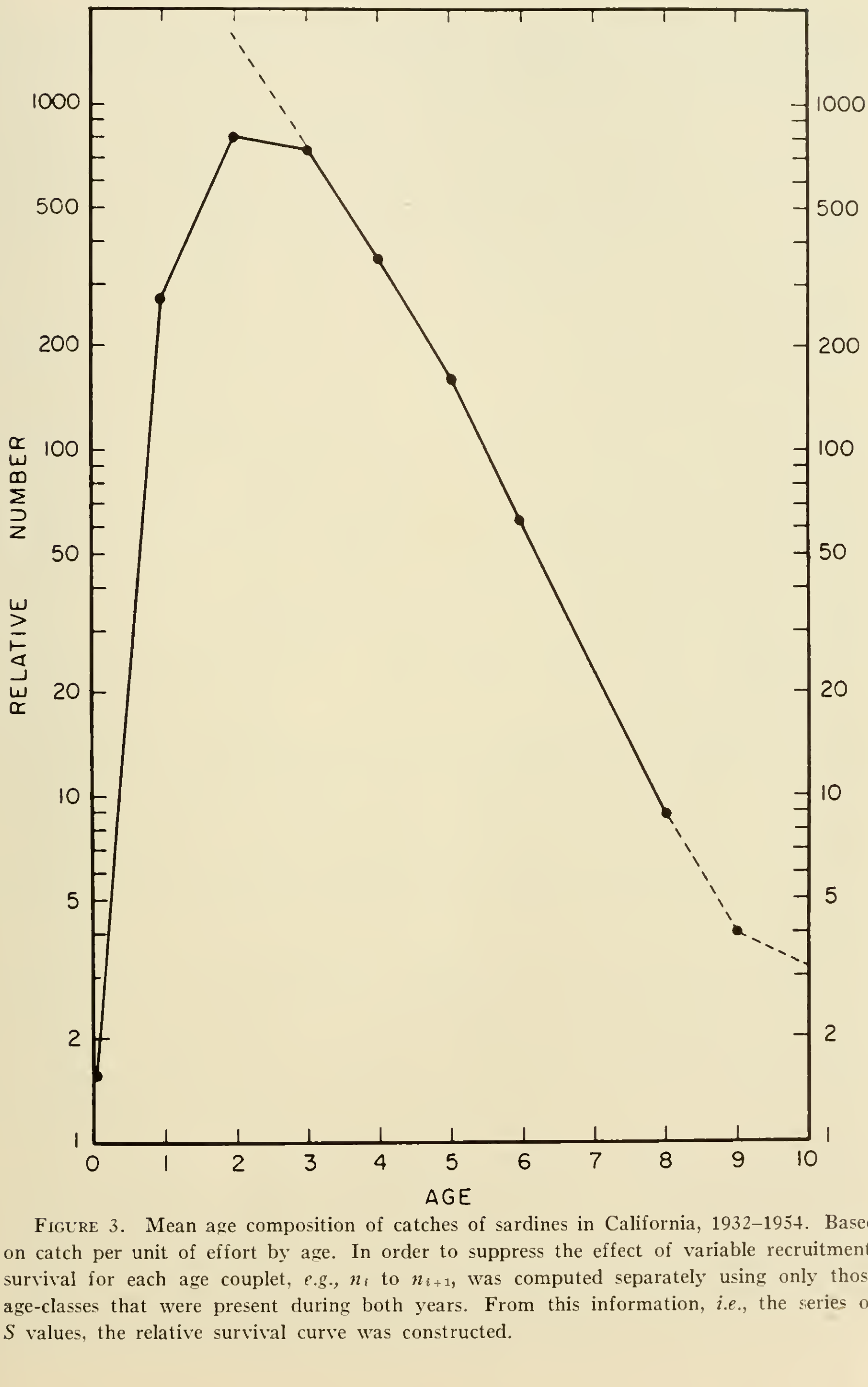

Figure 3. Mean age composition of catches of sardines in California, 1932–1954. Based on catch per unit of effort by age. In order to suppress the effect of variable recruitment, survival for each age couplet, *e.g.*, n_i to n_{i+1}, was computed separately using only those age-classes that were present during both years. From this information, *i.e.*, the series of S values, the relative survival curve was constructed.

TABLE 4. *Summary of numbers per scouting night from Radovich (1952), tables 2 and 4, weighted by amount of coastline in each survey zone, together with commercial catches in thousands during the 1950–1951 fishing seasons.*

	Year Class								
	1951	1950	1949	1948	1947	1946	1945	1944	1943
1950	–	71,299	21,053	87,115	22,800	5,186	3,528	640	180
1951	48,089	20,964	14,089	50,094	7,097	1,433	466	–	–
Survival (S)	–	0.2940	0.6692	0.5750	0.3113	0.2763	0.1321	–	–
Coefficient of total Mortality (Z)	–	1.2242	0.4017	0.5534	1.1670	1.2863	2.0242	–	–
Catch (thousands)*	–	–	–	1,129,495	996,949	391,192	74,496	15,767	444

* 1950–1951 fishing season from Wolf, 1961, table 20, adjusted linearly for missing tonnage.

two adjacent year classes minimizes the possibilty of violating the assumption that the natural mortality of the two classes is the same. Perhaps even more important, consideration of only two adjacent age-classes (about 10 per cent difference in length) also maximizes the chances that the age-groups used in the computation are equally sampled by the surveys, since it seems likely that the effect of unknown factors such as age, specific changes in behavior, inshore–offshore distribution, etc., will also be minimized.

Equations 3.3 in Chapman and Murphy (1965) were solved for r_1 and r_2 using, from table 4:

$C_x = 996{,}949$; $C_y = 1{,}129{,}495$; $N_{x_1} = 22{,}800$; $N_{x_2} = 7{,}097$; $N_{y_1} = 87{,}115$; and $N_{y_2} = 50{,}094$. Natural mortality (M) was assumed to be 0.40. A value of 0.79 for F_x was obtained from table 1 in Chapman and Murphy (in press), with appropriate interpolation. That is, the mortality rate due to fishing of the 1947 (3-year-olds) year class during the 1950 season was 0.79. Equation 3.4 in Chapman and Murphy (in press) yields a value of $F_y = 0.17$, *i.e.*, the fishing mortality rate of the 1948 (2-year-olds) year class during the 1950 fishing season.

If the additional assumption is made that both surveys are representative of the real population, these determinations also can be used to estimate natural mortality from the information in table 4 by simply substracting the fishing mortality coefficients from the apparent total mortality coefficients. The result is $M = 0.38$ for both the 2- and 3-year-olds. (This numerical identity is the result of the assumption that M is equal for the two classes, and indicates nothing more than accurate arithmetic.)

(In introducing this method it was asserted that the solution was essentially independent of M. If the problem I have just treated is solved using an assumed M of 0.20 instead of 0.40, F for the 3-year-olds is estimated at 0.78 and M is estimated by subtraction at 0.39, clearly supporting the assumption.)

It is of interest to compare the natural mortality computed by the survey

technique ($M = 0.38$) for the 1947 and 1948 year classes with the apparent total mortality (all natural, as the classes were not caught by commercial fishing) of the 1949 year class ($M = 0.40$) and the 1950 year class ($M = 1.22$). The close agreement between the natural mortalities of 1-, 2-, and 3-year-olds is reasonable, as they are similar in size and might be expected to have fallen prey to the same sources of mortality. The much higher figure ($M = 1.2$) for the 1950 year class might also be expected, as the fish which were only a few months old during the first survey, must have been susceptible to a much wider range of sources of mortality than the older, larger fish.

If there is no bias in the sampling, confidence limits can be set on the estimated fishing mortality rates following the method of Chapman and Murphy (1965). Their method requires that the samples be drawn from a Poisson distribution. It is highly unlikely that this is met in the case at hand because we are dealing with schooling fish and up to 100 were taken from each school. Nevertheless, some idea of the accuracy of the estimates can be obtained by using the method, and the additional data in Radovich (1952), tables 19 and 22. The results indicate a variance of 0.0052 (standard deviation = 0.072) for the estimate of F for the 1947 year class in 1950. This is minimal, as Radovich did not directly age all of his samples. Judging by his text, only one-tenth were aged. If the published sample numbers (Radovich, 1952, tables 19 and 22) are reduced by this amount, the variance and standard deviations are 0.052 and 0.23. These latter estimates are probably closer to reality and they are disconcertingly broad. Relevant to the reliability of these estimates, it can be deduced from Radovich's data that some 95 separate samples were taken in 1950 and 66 in 1951, again indicating the broader confidence limits are closer to reality.

If it could be assumed that two's, three's, and four's are randomly distributed among schools and are randomly taken from each school (not too unreasonable because of their similarity in size), then nine-tenths of the information obtainable from these cruises was discarded by not aging all of the fish. This assumption almost certainly applies to the three's and four's, and it is worth noting that about two-thirds of the total variance just noted results from the small number (about 38) of 4-year-old fish aged from the 1951 survey. Clearly, additional consideration of the sampling problem can increase the usefulness of such surveys.

Despite the uncertainties surrounding the estimates, they supply information in addition to that provided by the catches and, hence, are of value in controlling the analysis of the catches. Of the several values derived from the survey data, only the fishing rate for 3-year-olds during the 1950 season, $F = 0.79$, will be used in subsequent computations. Parenthetically, some support has been obtained for the value of natural mortality ($M = 0.40$) deduced from the reexamination of Silliman's estimate.

Estimates by Other Investigators

A number of estimates of fishing and natural mortality rates are to be found in the literature. The potentially most useful of these resulted from tagging conducted over the period 1937 to 1945 (Clark and Janssen, 1945; Janssen, 1948). The raw data are not available so consideration is confined to published analyses. In all, 121,000 sardines were tagged with the dual objectives of describing migrations and estimating population size. Clark and Marr (1955) estimated total mortality from the returns for each of 9 years (1937–1945). Their values ranged from 48 per cent to 87 per cent, with a mean of 66 per cent (corresponding Z values 0.65–2.04, mean 1.08). From the same data, Clark and Janssen (1945) estimated the exploitation rate (E) over this period at 39 per cent to 50 per cent ($F = 0.49$–0.69), depending on the analytical method used, though they believe the higher value represents the best estimate. These same authors estimated the annual natural mortality rate (D) as 22 per cent to 36 per cent ($M = 0.27$–0.45). If their "best estimate" of the coefficient of fishing mortality ($F = 0.69$) is subtracted from the mean total mortality coefficient ($Z = 1.08$), an estimate of $M = 0.39$ is obtained.

Hart (1943, 1944), in summarizing the returns from 20,000 sardines tagged in British Columbia, Washington, and Oregon waters over 6 years (1936–1941), and recaptured along the entire Pacific Coast, estimated total mortality at 69 per cent ($Z = 1.17$), in close agreement with the average for the California experiments of 66 per cent. He made no attempt to separate this into fishing and natural mortality.

Though the above results seem to me to be the most substantial in the literature, other estimates have been made. Using other assumptions with respect to migration, Marr (in Clark and Marr, 1955) estimated from California tagging results for the same years, natural mortalities of 33 per cent and 39 per cent ($M = 0.40$ and 0.49), and fishing mortalities of 22 per cent and 28 per cent ($F = 0.25$ and 0.33). No combination of these, however, adds up to the observed total mortality coefficient of $Z = 1.08$, the most reliable statistic derived from the tagging data.

Marr (1960, p. 728) developed an estimate of natural mortality for fully recruited fish (presumably 3 years and older) for 7 of the 8 years during the period 1950 to 1957. His estimates varied from $M = 0.25$ in 1950 to $M = 3.91$ in 1952. He arrived at these by estimating the total population from egg surveys which, according to Taft (1960), have 95 per cent confidence limits ranging from about half to double the mean. He assumed that each female spawned 100,000 eggs and that there was a sex ratio of 1.0 (Phillips, 1948). Fishing mortality was estimated from the ratio of the catch to the population estimated from egg surveys, and this was subtracted from total

mortality estimated from the number of fish taken in year $n + 1$ divided by the number taken in year n, yielding natural mortality. A major source of difficulty, acknowledged by Marr, is that changes in availability from year to year could severely effect the estimates of survival (S), even if his implicit assumption of constant fishing effort were valid. In fact, the change in availability (or fishing effort) from 1953 to 1954 was such as to give an apparent survival considerably larger than 1.0, precluding any estimate for that year.

An additional difficulty with his approach is inherent in the timing of collection of his data. The sequence is (1) spawning stock estimate, (2) catch during fishing season, (3) spawning stock estimate, and (4) catch during fishing season, *i.e.*, the population size is estimated at time 0 but mortality is estimated between times 0.5 and 1.5. Thus, the numbers do not fit the time sequence inherent in his analytical model. Furthermore, he treats the spawning stock as if it were $\overline{N}$, whereas it is much closer to N_0. This causes him to underestimate fishing mortality, perhaps by as much as 60 per cent, and overestimate natural mortality. His estimate of fishing mortality is further reduced because the spawning stock includes all 2-year-old fish (Ahlstrom, 1960), but these are only partially recruited. It appears impossible, analytically, to derive a reliable estimate of M by this approach, and it seems certain that the figures derived are considerably higher than reality.

Yamanaka (1960) has also calculated coefficients of natural mortality for the Pacific sardine, though he does not give the details of his methods. His values range from 0.10 to 0.75; those based on analyses of virtual population (Fry, 1949) are 0.34 and 0.40.

Table 5 summarizes those estimates of natural and fishing mortality coefficients for the Pacific sardine population that I believe are most reliable.

Holt (1960) has assembled a number of estimates of natural mortality (M) from populations of different species of *Sardinops*. They are of interest as the ecological framework for other sardine populations may be similar. They range from 0.15 [the early estimate derived by Silliman (1943)] to 0.9 (Nakai, 1960). Yamanaka (1960) lists three estimates of natural mortality (M) for the Japanese sardine. The more substantial of these are 0.3 (from tagging) and 0.5 (from catch and effort statistics). For the same population, Nakai (1960) gives estimates ranging from 1.3 to 0.9. However, his method appears similar to that of Marr (1960) and his estimates, therefore, include the same sources of error.

In a more general paper, Beverton and Holt (1959) found that natural mortality coefficients for Clupeidae range from 0.2 to 1.2. Natural mortality coefficients of 0.2 or even 0.4 may seem absurdly low for such small fish. They are consonant with reality, however. For example, the extraordinarily successful 1904 year class of Norwegian herring contributed significantly to the

Table 5. *Mortality coefficients for the Pacific sardine.*

Period	*Rate*	*Method*	*Value*
1937–1945	Natural (*M*)	Silliman	0.34
1937–1945	Natural (*M*)	Silliman	0.42
1937–1945	Fishing (*F*)	Silliman	0.68
1937–1945	Fishing (*F*)	Silliman	0.60
1950	Fishing (*F*)	Survey-Catch	0.79
1937–1945	Total (*Z*)	Tagging	1.08
1937–1945	Fishing (*F*)	Tagging	0.69
1937–1945	Natural (*M*)	Tagging	0.39
1936–1941	Total (*Z*)	Tagging	1.17

fishery from 1907 to 1923, a period of 17 years (Hardy, 1959). In the instance of the sardine, about 1 per cent of landings during 1932–1934 was 13 or more years of age. Taken at face value, this suggests a coefficient of total mortality (Z) of around 0.50, which, of course, includes both natural and fishing mortality.

POPULATION ESTIMATES

Egg Surveys

Surveys for pelagic eggs by systematic towing of plankton nets over spawning grounds have a long history. One of the earliest comprehensive studies in the United States was conducted in 1932 over the spawning grounds of the Atlantic mackerel (Sette, 1943). The earliest such study on the Pacific sardine was reported by Scofield (1934). This study attempted to delineate the time and place of spawning. Further surveys conducted in 1939–1941 had as a restricted objective the estimation of the total number of eggs spawned in the waters off southern California (Sette and Ahlstrom, 1948). The success of this attempt, which involved sampling over a fixed grid several times during a spawning season, together with the dramatic decline in sardine landings led to reestablishment of the surveys on a vastly expanded scale in 1949. From these expanded egg and larva surveys, it was hoped to obtain quantitative annual estimates of larval survival and estimates of population size. The latter is of concern here.

Very briefly, the egg and larva surveys consisted of a systematic pattern of meter-net plankton stations designed to embrace the entire spawning range of the sardine (roughly Monterey to the southern tip of Baja California), and extending from about 2 miles off the coast to 200 miles offshore. The stations were occupied at approximately monthly intervals. Details of methods and results are given in papers by Ahlstrom (1954, 1959a), as well as in a series of data reports. The last of these published covers the 1957 surveys

(Ahlstrom, 1959b) and provides references to all those preceding it. Two questions arise if one uses the results of these studies for deriving population estimates: What is the relation between the estimated total number of eggs spawned and the population biomass? And what are confidence limits for the estimates?

There are two published studies relevant to the first question (Clark, 1934; MacGregor, 1957). There are some areas of agreement between these studies, *e.g.*, the number of eggs spawned at a single spawning by certain sized fish, but there are important differences. Clark's material was collected mostly from 1928 to 1931, and MacGregor's, in 1945 and 1946. In addition, as pointed out by MacGregor, Clark had material from all months of the year, and MacGregor had material only from November through February. Since there is considerable evidence that the period of spawning shifts, there is a good chance that MacGregor's material was even earlier in the "biological year" than suggested by the calendar dates. Furthermore, he was unable to examine ovaries during the spawning season, or from a wide geographical range. There are also differences in the way the data were treated. Clark (1934) used the ratio of the numbers of eggs from 0.20 to 0.59 to those over 0.59 mm. as one criterion of the potential number of spawnings. MacGregor used the ratio of the number in the largest modal group as the denominator and the number of smaller eggs larger than 0.20 mm. as the numerator. This could easily account for at least part of their differences. In addition, MacGregor computed his ratio as an average of ratios and Clark computed hers from the summed numerators and summed denominators. MacGregor's method may have introduced considerable bias, as it gives equal weight to fish that are producing many eggs and to fish that are doing poorly in terms of fecundity, and, therefore, might be expected both to mature a small batch of eggs and deposit a smaller number of batches.

MacGregor (1957) believed, on the basis of his samples, that not more than 2.5 batches could be spawned, but felt that even this number was uncertain. He states:

> No conclusions can be drawn from the material used in this study regarding the number of groups of ova that a sardine will spawn in one spawning season. The evidence presented in the literature by various authors is inconclusive and their conclusions are contradictory.

One of the points at issue is whether there is time for more than one spawning. MacGregor offers evidence that, for example, in 1951, 97.2 per cent of the spawning off southern California occurred within a 2-month period. This is true, but Ahlstrom (1959a) showed that in 1951 only 2.5 per cent of the total spawning occurred off southern California. If the total spawning range is considered, there was substantial spawning throughout a 9-month period.

On the basis of the preceding information, I am inclined to accept Clark's

conclusion that an average of three or more batches of eggs are spawned per year by the Pacific sardine.

MacGregor's careful determination of the relationship between number of eggs per spawning and fish weight is consistent with Clark's data. He estimates from regression analysis that there are 263 ova per gram weight of sardine per batch, which, accepting three as the number of spawnings and equal representation of males, yields 395 ova spawned per gram of spawning population biomass.

Both authors' data suggest that during the period of their studies (1928–1946), roughly half the 2-year-olds and all of the older fish spawned. New data presented by Ahlstrom (1960) show that for the 1950's, it is more realistic to consider all of the 2-year-olds as mature and spawning. This change appears to be associated with the more southern distribution of the population in the 1950's.

Taken all together, there is enough information to attempt to estimate spawning stock biomass from the egg surveys. In using these data, I will assume all fish 2 years old and older spawned, and that every 395 eggs in the sea represents 1 gram of spawners (male and female).

There remains the problem of placing confidence limits on the results of the individual surveys. The first study of this problem (Silliman, 1946) was based on a comparison of consecutive hauls, *i.e.,* a second haul was made on a series of stations as soon as the cod end plus the sample of the first haul were removed and replaced. Silliman's analysis of these "paired" samples showed that the variance was proportional to the mean and that the counts could be "normalized" by a log transformation. Sette and Ahlstrom (1948) used Silliman's estimates of within-station variance as the basis for setting confidence limits for an entire cruise of many stations. Under these conditions, a single station must be treated as representative of a 40- to 60-mile square, and it seems unlikely that the limits Silliman derived are applicable. If they are not, Sette and Ahlstrom (1948) overestimated the precision of the surveys.

Taft (1960) reexamined the problem and estimated the reliability of a single haul with respect to a 400-square-mile area on the basis of special grids of stations 4 miles apart. His results showed that the distribution of the counts could be described by a negative binomial, and that the 95 per cent confidence limits of each of the survey cruises he examined were roughly half to double. In trying to extrapolate his results for a single cruise to a season's cruises, *e.g.,* 12 monthly cruises, Taft (1960) expressed concern that new and unevaluated sources of variability might be introduced and not be reflected in the estimate of variability of the observations. Evidently, he was concerned over such problems as estimating the variability introduced by a periodic phenomenon (spawning), by means of measurements evenly

spaced in time (cruises). This would not be of concern if the cruises were randomly placed on the time axis. Even with regularly spaced cruises, the effects of the lack of randomness are reduced by the temporal variation of the events being measured. That is, judging by the maturity of the fish themselves and the results of the egg surveys, there seems to be no overall population synchrony; at a particular time and place, only a relatively small portion of the population spawn.

The fact that there were only 10 to 12 cruises does not, I believe, introduce serious difficulties in regarding a year's cruises as a continuum of observations, unbiased with respect to the locale and periodicity of spawning. This is because it takes about 3 days for eggs to hatch, so that each sample cruise is representative of about one-tenth of a month, and because the cruises were not synoptic but lasted from 2 weeks to a month.

As the egg samples seem to be drawn from a negative binomial, an appropriate transformation (Anscombe, 1948) would be:

$y = \log_{10}(x + \frac{1}{2}k)$ where (k) is the contagion coefficient of the negative binomial. However, the three cruises studied by Taft (1960) yielded estimated k's ranging from 0.14 to 0.76 and I propose to ignore this small correction. This should increase the calculated variance only slightly, an effect that can be offset by ignoring all zero values even when they are within a clearly delineated spawning area. Their interpretation is questionable, *i.e.*, whether they reflect no spawning in the grid square or sampling, and they are relatively few (20–30 per cent). Trial calculations assuming 20 per cent zero observations show that this procedure underestimates the confidence limits by about 5 per cent.

Turning now to the results of spawning surveys from 1951 to 1958, there is an additional decision to make concerning the so-called late spawning. Well over 99 per cent of all spawning during these years occurred in the area from Point Conception to the southern tip of Baja California. During the period from January to June, spawning was heavy throughout the entire region. In the southern part, Sebastián Viscaíno Bay to the tip of Baja California, there was a second spawning peak in the July-to-September period. The problem is, does this latter spawning represent part of the three spawnings a year that Clark (1934) clearly showed could occur throughout the range, or does it represent additional spawning (more than three times a year) by a segment of the population in response to the more protracted period of warm water in the south. I prefer the second alternative because Clark's results showed that more than three spawnings could occur, and will, therefore, only consider the eggs collected between January and June, inclusive. Table 6 shows the estimated total number of eggs deposited during this period, the estimated tons of spawners, using the relationship already discussed of 395 eggs per gram of spawning population, and the 95 per cent confidence limits, based

TABLE 6. *Summary of egg estimates and derived population statistics.*

Year	Estimated Eggs (billions)	Spawning Population (short tons)	95 Per Cent Confidence Limits (in per cent)	Catch (short tons)	Apparent Fishing Rate	Apparent Mortality Coefficients	
						F	Z
1951	531	1,481,000	70–143	145,288	0.098	0.13	0.53
1952	109	304,000	67–150	14,873	0.049	0.06	0.46
1953	89	248,000	78–128	18,798	0.077	0.10	0.50
1954	296	826,000	74–136	80,905	0.098	0.13	0.53
1955	147	410,000	68–148	78,668	0.190	0.26	0.66
1956	162	452,000	55–180	47,298	0.104	0.12	0.52
1957	44	123,000	66–151	32,196	0.260	0.37	
1958	80	223,000	86–117	126,305	0.565	1.09	
1954–1958		2,034,000					
1951–1958		4,067,000					

on a $\log_{10}$ transformation of all positive stations. The estimated total spawning population for the years 1954–1958 is included because it is required later in the analysis. The actual catches will then be considered in relation to the estimated population.[1]

CHANGE IN NATURAL MORTALITY RATE

Solutions of equation (14) for each year in the period 1932–1960 were obtained using the catch data (yet to be presented) and an assumed natural mortality rate of $M = 0.4$. For the years prior to 1950, the solutions were consonant with all additional information on the population. There were, however, major conflicts with respect to the period after 1950: (1) if a solution were obtained that was consonant with the pre-1951 information and with the total mortality prevailing during the 1950's, the total population from that solution was smaller than that indicated by the egg studies by a factor of 3; (2) solutions less consonant with the pre-1951 information, but still within reason, and yielding population estimates fully consonant with the average 1954–1958 population indicated by the egg surveys, yielded unrealistic results for the 1951–1960 period.

First, they indicated an increasing rather than decreasing population, and second, they yielded total mortality estimates incompatible with observed longevity. This difficulty was resolved by increasing the natural mortality coefficient (M) to 0.8 for the 1950's. Prior to making this decision other

[1] After this study was completed it was learned that the 1950 egg surveys, while deficient in some respects, afford an estimate of the numbers of sardine eggs spawned. The spawning population for that year was estimated at 716 thousand tons independently of the egg data. Based on 395 ova per gram of spawner and three spawnings, January to June inclusive, 313×10^{15} eggs should have been deposited. Ahlstrom's estimate from plankton samples is 256×10^{15}. This is close agreement considering the confidence limits, and, parenthetically, one spawning per year is well outside the 95 per cent limits.

possible sources of the discrepancy were examined in some detail. These will now be discussed.

The methods of sampling the catch for aging will be given further consideration in a later section. Pertinent here is the possibility that the catch records for the early 1950's might be enough in error to give misleading results, because of small landings, *e.g.*, 15,000 tons in 1952 with a significant fraction of them made in Baja California where it was not possible to sample thoroughly. The extreme would be that unrecorded catches in Mexico were as large as the combined recorded United States–Mexico catch, but there is no evidence that any significant number of Mexican landings were unrecorded. The effect of possible sampling errors in the catch records was explored by various methods of weighting the aged catches during the 1950's. None of these schemes substantially altered the results.

During the 1950's, the fishery operated off California and Baja California (table 1). In Baja California, landings occurred off Ensenada during the early 1950's and gradually shifted southward (table 7). The location of capture shifted southward even more rapidly than the port of landing (table 8). This suggests the possibility that the fishery landings were not drawn from the same population as the egg samples, and that the landings might reflect a more restricted segment of the population than egg surveys, which were designed to cover the entire population. The pattern of the fishery and tagging experiments, however, indicate that this is probably not so.

For example, as the fishery shifted south, there was no indication that it was drawing on previously unused stocks (table 13). The age composition of the southern landings was similar to that of the northern landings, and if the southern fish had not been previously fished, one would have expected a larger fraction of older fish in the population.

The conclusion that the fishery during the 1950's was drawing from the entire population is also supported by tagging results (Janssen, 1948; Clark and Janssen, 1945; Clark and Marr, 1955). One fish tagged off Baja California was recovered as far north as the Pacific Northwest (one return). More to the point, the relative rate of return of tags from fish released during 1941 in Sebastián Viscaíno Bay (Cedros Island area) from the southern California fishery was higher than for releases in any other area (Clark and Marr, 1955, tables 6 and 7). These results strongly suggest that a fishery based even as far north as Ensenada, Baja California, will draw on the entire population.

There is some internal evidence of a change in the natural mortality coefficient (M). The information in table 6, page 28, together with the age composition of the landings denotes total mortality, *i.e.*, natural mortality plus fishing mortality. One way to consider the problem is to compute the average Z for the period 1951 to 1956 when the exploitation rate (E) was low (table 6), on the basis of the apparent fishing rate and assuming the earlier estimate

Table 7. *Baja California catches by points of landing. Unpublished data from the files of the Bureau of Commercial Fisheries.*

Year	Total Tons	Per Cent of Total Landed at: Ensenada	San Quintin	Cedros Island	Puerto Adolpho Lopez Mateos
1951	16,184	99	–	1	–
1952	9,162	87	–	13	–
1953	14,306	86	–	14	–
1954	12,440	94	–	6	–
1955	4,207	91	–	9	–
1956	13,655	90	–	10	–
1957	9,924	90	–	20	–
1958	22,334	70	4	26	–
1959	21,424	59	7	34	–
1960	19,899	49	2	49	–
1961	19,842	49	–	51	–
1962	16,198	35	–	27	38
1963	19,390	28	–	37	35

of $M = 0.40$ still holds, and from this calculate an expected age composition. This distribution can then be compared with the observed age composition of the catches during 1957 and 1958. That is, if natural mortality (M) were really as low as 0.40, this, coupled with a low rate of exploitation (E) for 6 years, should have been reflected in the age distribution of the catches, especially longevity, during the 1957 and 1958 seasons.

The "computed" average mortality for the 1951 to 1956 period is $\bar{Z}_{51\text{-}56} = 0.53$. From this, a schedule of expected age composition has been computed and tabulated (table 9), together with the observed age compositions in 1957 and 1958. These results clearly indicate that the expectation of survival is considerably less than if the apparent fishing rates (table 6) and the assumed natural mortality coefficient of 0.40 had held. Little more can be derived from this approach because the observed age composition reflects year class strength as well as survival. It is likely, however, that any bias

Table 8. *Baja California catches by area of capture. Unpublished data from the files of the Bureau of Commercial Fisheries.*

Year	Total Tons	Per Cent of Total Captured Near: Ensenada	San Quintin	Cedros Island	Puerto Adolpho Lopez Mateos
1961	19,842	8	–	92	–
1962	16,198	16	–	46	39
1963	19,390	13	–	52	35

TABLE 9. *Per cent distribution of age classes, 3 years and older. Expected in the catch, if the average total mortality ($\bar{Z} = 0.53$) derived from table 6, p. 28, and assumed rate of* M = *0.40 had held, compared with the observed values.*

Age	*Expected Per Cent* M = *0.40*	*Observed 1957*	*Year Class*	*Observed 1958*	*Year Class*	*Expected Per Cent* M = *0.80*	*Mean Per Cent 1957, 1958*
3	41	47.1	54	80.1	55	61	64
4	24	23.7	53	12.1	54	24	18
5	15	23.5	52	5.2	53	10	14
6	8	4.6	51	2.1	52	4	3
7 and older	12	1.1		0.5		2	1

from this source strengthens the argument because all other measures strongly indicate that the 1954 and 1955 year classes were weaker than some of those preceding them, *i.e.*, 1951 and 1952.

Another way to examine this point is to compare the virtual populations (Fry, 1949) with the estimates from egg surveys. For the period 1951 to 1957, the former are only about one-tenth the size suggested by the egg surveys, again indicating a value of F close to 0.1, which is not consistent with longevity in 1957 and 1958 if $M = 0.40$.

The remaining possibility for reconciling the observations is to assume that the sardine spawns more often than the assumed three times a year. Clark's (1934) data suggest that this might be true, and it was on this basis that only eggs spawned during the main spawning period (January through June) were used in deriving the population estimates. Reconciliation with a natural mortality coefficient (M) of 0.40 requires postulating nine spawnings during the 6-month period. This seems unreasonable. Solutions involving intermediate results could be entertained, but to a considerable extent the final results would not be altered because of the compensatory nature of the solution. That is, if I have overestimated the population, I have been forced to dispense with them by postulating a higher rate of natural mortality in order to obtain mortality rates consonant with the observed age structure.

The final decision is clearly somewhat subjective, but in the light of all information the most reasonable decision seems to me to be to assume three spawnings during the January-to-June period and increase the natural mortality rate to 0.80.

RACES AND OTHER ASPECTS OF THE SARDINE POPULATION

Prior to taking up the numerical evaluation of the population, there are

additional factors that must be considered concerning the biology of the sardine. Some of these are directly relevant to the numerical evaluation, while others are required to understand and interpret the results.

SUBPOPULATIONS

The possibility of the existence of races or subpopulations of the Pacific sardine has received continuing attention since Hubbs' (1925) study. Aside from general interest, the problem is especially important with respect to exploited species as it is desirable to consider each major population unit separately, whether or not they are all harvested more or less equally by the fishery. Clark (1947) compiled and reviewed all of the available data on vertebral number. She concluded that there was some basis for regarding the population in the Gulf of California and the most southern part of Baja California as racially separate from a more or less freely intermingling population to the north.

Wisner (1961) has compared Clark's vertebral counts with data gathered over the period 1951 to 1957. His evidence confirms Clark's findings for the Gulf of California, but, excepting the lowermost part of Baja California, the later vertebral counts are lower than those of the earlier period. Wisner suggests that there has been a change in the "racial" mixture supporting the fishery, and, more specifically, that a northern race (more vertebrae) has declined disproportionately with respect to a southern race.

More recently, the results of subpopulation studies using erythrocyte antigens has led to the delineation of genetic strains of sardines (Sprague and Vrooman, 1962; Vrooman, 1964). The results of these studies agree with the results based on vertebral counts. However, as blood characters are thought to be completely genotypic in origin, serological studies can provide more useful information. The workers were able to identify samples (schools) unambiguously as belonging to one race or another.

Vrooman (1964) reports that the population of sardines is made up of three races. One, in the Gulf of California, is apparently restricted and is not involved in the Pacific Coast fisheries. The other two are involved. The southern race has been identified from southern Baja California to San Pedro; those from the northern race, from San Quintin in northern Baja California to Monterey. The apparent wide overlap in distribution of these races is due to integration over time. Apparently their north–south movements are synchronous because they have not been found overlapping during any particular survey. Their genetic identity also argues for effective separation at spawning.

The movement of fish deduced from tag returns (fig. 4) is also compatible with the results of the serological studies. The movements of the sardines, as shown by the tag returns and by the timing of the fishery along the coast, were summarized by Clark (1952, p. 373):

> By the end of their first year they have evidenced a slight northwward movement and in each succeeding year this northward migration becomes more pronounced. These northward movements occur during the summer months and a return southward takes place in the late fall and winter . . .

This seasonal movement has also been noted from the serological studies, *e.g.,* a southward shift of the northern population during the fall and winter, and fish tagged in Sebastián Viscaíno Bay (southern race) were mainly recovered south of Point Conception.

During the 1961 fishing season, it was possible to relate the commercial catch to specific subpopulations. The data indicate that all the landings in southern California were from the northern race and all those in Baja California were from the southern race. There were differences in the relative strength of the various year classes in catches from the two areas, and fish of the same age from the Baja California fishery were markedly (about 30 percent) shorter in mean length than those from the southern California fishery. This clearly indicates either genetic differences in growth characteristics, or the effect of different environmental conditions, or both (Vrooman, 1964).

Résumé of Population

Except for the 1961 season, the commercial catches, which are essential to the balance of this study, cannot be identified with respect to race. I will, therefore, assume that there were, during the entire 1932–1960 period, two genetic races of sardines, a southern and a northern. The northern race was the larger of the two as judged by the fact that up to 1945, landings north of Point Conception were two to three times larger than those to the south (table 1), while tag returns indicate that fish almost certainly of the southern race did not contribute heavily north of Point Conception.

The landing pattern and tag returns also indicate that by the late 1950's the relative strength of the two races was reversed. Landings during the 1954–1960 seasons were mostly from south of Point Conception, the ratio being 5.8 : 1. This is close to the ratio (6.1 : 1) of recoveries to the north and south of Point Conception for fish tagged in Sebastián Viscaíno Bay (Janssen, 1948).

That a change occurred in the proportion of the races between the two eras is clear. In order to examine the population size within the analytical framework, a decision must be made as to which year class was the first to become predominantly southern instead of northern. I have selected 1949 because this was the first cohort to be relatively unavailable north of Point Conception and, to a lesser extent, at San Pedro, but was relatively available to the Ensenada fishery.

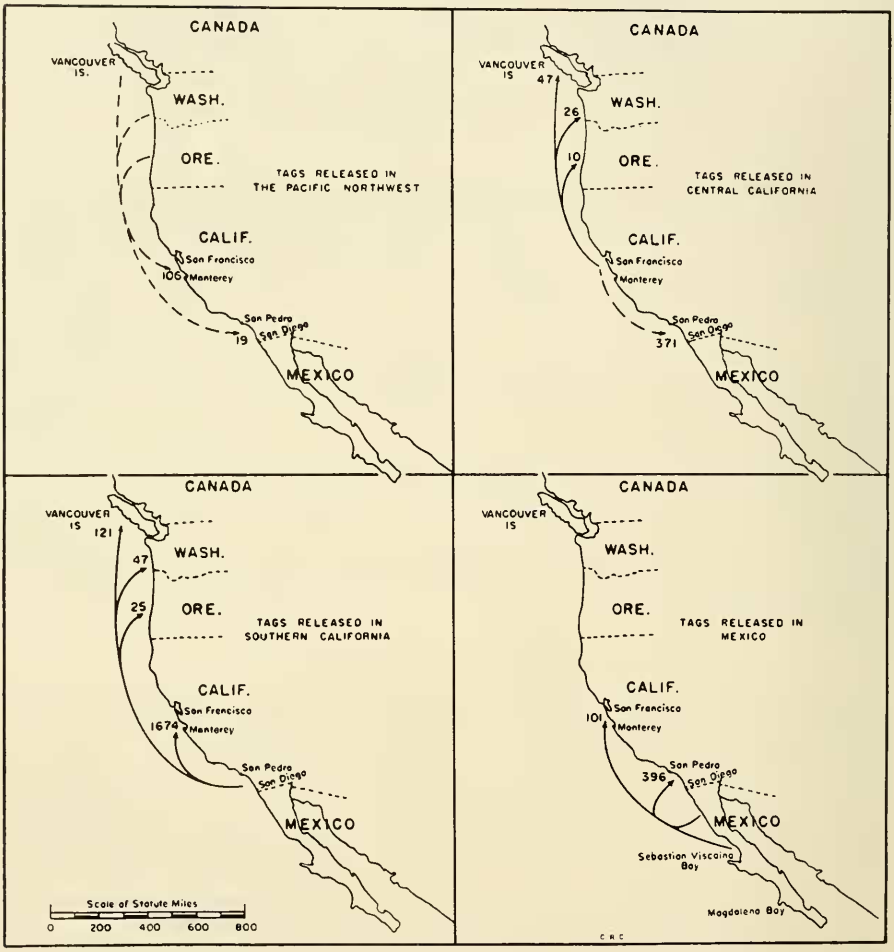

FIGURE 4. Sections of the Pacific Coast of North America showing diagrammatically the major movements of tagged sardines as indicated by recoveries from June, 1935 to May, 1944. (From Clark and Janssen, 1945.)

A natural mortality coefficient of $M = 0.40$ applied to the population subject to the fishery before the 1949 year class appears to give reasonable estimates of the population. After the 1949 and subsequent year classes dominated the population (1954 ff.), a natural mortality coefficient of $M = 0.80$ gives more reasonable estimates. This change is, of course, coincidental with the change in distributional pattern of the fishery described above. In solving for the population using equation (15), page 12, the transition was accomplished by treating the 1949 and subsequent year classes separately.

It cannot, at the present time, be quantitatively demonstrated why the southern stock should have a higher natural mortality coefficient. However, some qualitative suggestions can be made. They are smaller at a given age (Vrooman, 1964). Even by their fifth year they have not achieved the size of 2-year-olds of the northern race. This should make them susceptible to a broader spectrum of predators. Furthermore, the sort of fish that would be expected to prey on the sardine are more abundant off Baja California. For example, yellowfin tuna and skipjack tuna annually migrate into the region in large numbers (Broadhead and Barrett, 1964). The population of yellowtail, *Seriola dorsalis* (Gill), appears to center off Baja California (Baxter, 1960) and sardines are taken in significant numbers by this species.

Because there is no way of separating the two races in the commercial landings for the period 1932–1960, the estimates that are developed on the basis of the landings do not represent a population in a strict biological sense. They refer to mixtures and the implicit assumption in treating them as units is that, within each of the two periods, *i.e.*, year classes up through 1948 and year classes from 1949 on, the relation between abundances of the two races and their relative contributions to the catches were constant though unknown.

EVALUATION OF THE POPULATION FROM THE CATCHES

Numerical Solution

The basic data required for solving equation (15) are the age structure of the population for each year and the total numbers landed. The total tonnage of sardines landed can be assumed to have been measured, and from this total numbers can be estimated. The problem of sampling the landings was considered in detail by Sette (1926), reviewed by Felin and Phillips (1948), and reexamined by Widrig (1951) as described in Felin *et al.* (1952). The basic sampling system involves obtaining grab samples of 50 fish several times a week from the landings at each port. All are measured, and 10 selected at random from each sample are aged. This information, together with the tonnage landed at each port, can be used to obtain an estimate of the age composition of the total catch. Wolf (1961) has summarized the results of this sampling for the period 1932 to 1960.

In addition to the catch record, estimates of total effort and catch per unit of effort presented in Clark and Daugherty (1952) for the period 1932 to 1950 have been utilized. Data for the period 1951 to 1960 either are not available or are not comparable to the earlier series (Clark, 1956), so a value of 1,527 units of effort, the last published value, was used for this period in order to use the same computer program.

The data in table 10 refer only to those ages used in solving equation (15). Ages less than three are not appropriate because they are not fully recruited (fig. 3). Fish older than six were not usually used because of

uncertainties in sampling and aging, and because their inclusion would, in most cases, have had little effect on the result. This rule was broken for the 1953–1955 period because it was felt that the inclusion of the older fish was a significant contribution to the information. The S* series required for equation (15) was derived from table 10 by dividing the numbers of fish of appropriate ages in year $n + 1$ by the appropriate numbers in year n. Usually, this involved dividing the numbers of 4- + 5- + 6-year-olds in year $N + 1$ by the numbers of 3- + 4- + 5-year-olds in year n. Because of the assumed change in natural mortality coefficient from 0.40 to 0.80 beginning with the appearance in 1952 of the 1949 year class in the fishery, it was necessary to compute two series of S^* values and solve for the population in two parts. The S^* series and the calculated statistics for the pre-1949 year class population are shown in table 11; those for the post-1949 year class population are shown in table 12.

The extra information needed to solve the earlier series was the estimate of F for 1950, 0.79, derived earlier from survey data, and $M = 0.40$. To the extent that effort (f) was measured accurately the r values in table 11 for the years 1932 to 1950 probably represent real changes in the efficiency of the fleet from year to year, induced either by operational changes or variations in the availability of the fish. For the years 1951 to 1960 when an arbitrary value of effort (1,527) was assumed, they are simply computational artifacts. The statistic E when divided into the measured catch provides an estimate of the population at the beginning of the fishing year.

Because the data in table 12 are, in effect, an independent series covering 9 years, two new sources of extra information are required. The first was supplied by the estimate of mean population, 1954–1958, derived from egg counts. A second, equally objective, degree of freedom was not available, so recourse was had to partially subjective criteria. The procedure was as follows:

Judging from the egg counts, the population was declining over the period (table 6), but solutions using $M = 0.40$, consonant with the S^* series (table 12) and yielding a mean population for the period that agrees with the 1954–1958 population estimates from the egg counts, indicated a rapidly increasing rather than decreasing population. This could be rectified by increasing M. As already indicated, $M = 0.80$ was finally selected. The case of $M = 0.90$ was also studied, but at this value, in order to reach agreement with the mean from egg studies, fishing effort in 1960 would have had to approach infinity. In order to keep the mean of the entire series (1954–1958) near the mean estimate for those years from egg counts, it was necessary to select solutions with larger F's during the later years (*e.g.*, F_{60}). This agrees with the observation that fishing mortality was much lower in the earlier years (table 6). Successive trials indicated that an F_{60} value of 1.36

TABLE 10. *Catch data used to solve for population size. Values for 1932–1950 are measured by catch per unit of effort and total effort. Values for 1951–1960 are estimated catches and an arbitrary effort figure. Data for 1932–1950 prepared from Wolf (1961), table 20; and Clark and Daugherty (1952), table 7; except for 1938. The derivation of values for this year is discussed in Appendix 1. Data for 1951–1960 are from Wolf (1961), table 22, adjusted for missing tonnage.*

Year	Effort Boat Months	Numbers by Age*				
		3	4	5	6	7 and over
1932	448	1,058	995	386	171	–
1933	600	480	590	605	407	–
1934	717	1,644	685	397	394	–
1935	876	2,090	642	197	217	–
1936	1,237	790	1,548	663	129	–
1937	1,366	346	393	257	67	–
1938	1,399	504	105	121	72	–
1939	1,314	877	199	42	54	–
1940	1,125	1,002	267	45	20	–
1941	1,304	1,196	217	53	8	–
1942	1,010	1,717	704	159	52	–
1943	1,122	854	901	282	73	–
1944	1,305	573	446	423	146	–
1945	1,315	634	363	149	71	–
1946	1,485	251	93	34	6	–
1947	1,358	126	65	36	9	–
1948	921	177	63	17	2	–
1949	947	813	239	118	14	–
1950	1,527	648	254	48	10	–
1951	"1,527"	781	180	63	15	–
1952	"1,527"	23	56	14	4	–
1953	"1,527"	40	12	50	4	1
1954	"1,527"	231	74	44	65	6
1955	"1,527"	270	142	25	11	22
1956	"1,527"	93	119	28	4	–
1957	"1,527"	80	36	34	6	–
1958	"1,527"	265	52	21	9	–
1959	"1,527"	221	31	2	1	–
1960	"1,527"	221	67	6	–	–

* 1932–1950 thousands per boat month. 1951–1960 millions per fishing year, as effort data are not available. In actual computation, three more digits than given here were employed.

would serve to anchor the later years. Although the selection of F_{60} and M were somewhat arbitrary in detail they were not entirely so, since the solutions have a number of constraints; *e.g.*, the S^* series, and the actual catches. Furthermore, this treatment of the year classes subsequent to 1948 did not introduce any obvious discontinuities in the population as a function of time.

TABLE 11. *Statistics on the sardine population 1932 to 1955 from solution of equations 15, 17, and 18, based on the 1948 and earlier year classes.* $v = 0.0008898$, $M = 0.40$. S^* *derived from table 10.*

Year	*Effort* (f) *Boat Months*	*3 Years and Older*				*2-Year-Olds*
		Availability				
		S*	r	F = rvf	E[a]	F
1932	448	0.6567	0.2627	0.1047	0.0824	0.0376
1933	600	0.8813	0.2925	0.1562	0.1197	0.0544
1934	717	0.3871	0.4810	0.3068	0.2201	0.0778
1935	876	0.7988	0.3750	0.2923	0.2107	0.1857
1936	1,237	0.2393	0.7492	0.8247	0.4756	0.2219
1937	1,366	0.3229	0.5818	0.7071	0.4276	0.4031
1938	1,399	0.3746	0.5686	0.7077	0.4280	0.5214
1939	1,314	0.3050	0.6626	0.7747	0.4559	0.4698
1940	1,125	0.2100	0.6122	0.6128	0.3854	0.2063
1941	1,304	0.6244	0.3192	0.3704	0.2580	0.3094
1942	1,010	0.4869	0.4344	0.3904	0.2696	0.2381
1943	1,122	0.4982	0.4856	0.4849	0.3218	0.2521
1944	1,305	0.4060	0.6585	0.7647	0.4518	0.5285
1945	1,315	0.1167	1.0000	1.1701	0.5902	0.5530
1946	1,485	0.2926	0.4457	0.5889	0.3740	0.4760
1947	1,358	0.3613	0.3219	0.3889	0.2690	0.1941
1948	921	1.4389	0.2346	0.1923	0.1449	0.3456
1949	947	0.2678	0.7344	0.6188	0.3882	0.4295
1950	1,527	0.2711	0.5858	0.7959	0.4643	0.3942
1951	"1,527"	0.0719	0.5009	0.6806	0.4163	–
1952	"1,527"	0.7482	0.0830	0.1127	0.0884	–
1953	"1,527"	1.2676	0.1051	0.1428	0.1103	–
1954	"1,527"	0.3026	0.2503	0.3401	0.2402	–
1955	"1,527"	–	0.1494	0.2030	0.1524	–

[a] E = the fraction of the decrease in population size over the year accounted for by removal by the fishery, *i.e.*,

$$E = \frac{F}{F+M}(1 - e^{-F-M}).$$

The catches of the fully recruited ages (three and over, table 13), when divided by the E values in tables 11 and 12, yield estimates of the populations of those ages. Using equations 16 and 17, the population of 2-year-olds can be estimated from that derived for the 3-year-olds plus the catch of 2-year-olds. The results are given in table 14. This procedure was followed except for the 1950 year class. During 1952 and 1953 this year class was so poorly represented relative to the others and in an absolute sense, that it was thought sounder to obtain an estimate by back-calculation on the basis of its estimated size in 1954, the first year it was well sampled by the fishery.

The computation using these values yielded results compatible with the

TABLE 12. *Statistics on the sardine population 1952 to 1960 on the 1949 and subsequent year classes from the solution of equation 15, and equations 16 and 17.* $v = 0.0008898$, $M = 0.80$. S^* *derived from table 10.*

Year	*Effort* (f) *Boat Months*	*3 Years and Older*				*2-Year-Olds*
		Availability				
		S*	r	F = rvf	E[a]	F
1952	"1,527"	0.5093	0.0265	0.0360	0.0244	0.0024
1953	"1,527"	2.2857	0.0312	0.0424	0.0284	0.0003
1954	"1,527"	0.5100	0.1806	0.2454	0.1520	0.1032
1955	"1,527"	0.3461	0.2765	0.3757	0.2211	0.1180
1956	"1,527"	0.3172	0.3170	0.4307	0.2479	0.0439
1957	"1,527"	0.5429	0.3505	0.4763	0.2689	0.0143
1958	"1,527"	0.0998	0.8964	1.2179	0.5233	0.6900
1959	"1,527"	0.2909	0.5762	0.7829	0.3931	0.4061
1960	"1,527"	–	1.0000	1.3587	0.5568	–

[a] $E = \frac{F}{F+M}(1 - e^{-F-M})$.

entire 1951–1958 egg series, *i.e.*, including years not entering into the 1954–1958 mean value used to derive a value of M. This involved combining the appropriate portions of the two series, and adding the 2-year-olds estimated from separate computations (formulas 16 and 17). From the egg data, the sum of the spawning populations (1951–1958) was estimated as $4{,}067 \times 10^3$ tons. My estimate for the aggregate of the period is $3{,}712 \times 10^3$ tons. This constitutes a secondary check on the procedure. As more information, *e.g.*, subsequent egg surveys and catches, becomes available, the solution summarized in table 12 can be reexamined.

It is pertinent to compare the values in tables 11–14 with other information and analyses not formally used in the computations. Estimates of average fishing mortality coefficient ($\overline{F} = 0.60$ and 0.68) for the years 1937–1945 were derived in calculating the Silliman estimate of natural mortality. These are close to the average of 0.66 for the same years (table 11). Using the results of tagging experiments and the model of Ricker (formula 7, 1944), Clark and Janssen (1945) computed an average exploitation rate (E) of 39 per cent for the period 1936–1943. This value is consonant with the average of 38 per cent for those same years developed independently in this study (table 11). Other ways of treating the tagging data, which appear to have less analytical validity, have yielded estimates of exploitation rate (E) ranging from 0.22 to 0.50 for this same period (Clark and Marr, 1955).

It is also appropriate to compare the results set forth in table 14 with virtual population estimates, as these underlie all previous attempts to understand the population dynamics of the Pacific sardine, except for those by

TABLE 13. *Total catches 1932–1960, Wolf (1961, table 22) adjusted for unsampled tonnage, and Wolf and Daugherty (1963) except for 1938. for this year see Appendix 1.*

Year	Numbers in Thousands at Age Indicated						
	2	3	4	5	6	7	8 and Over
1932	121,269	592,882	557,363	216,239	95,694	42,227	77,568
1933	379,773	307,620	378,497	387,834	261,098	122,747	298,733
1934	878,221	1,212,783	512,965	327,994	353,833	209,449	303,585
1935	575,826	1,855,794	578,911	208,765	246,820	103,911	161,346
1936	465,937	1,085,064	2,125,525	910,153	177,482	97,435	48,115
1937	1,491,410	647,753	734,888	481,727	126,298	64,418	22,948
1938	2,364,371	1,032,046	215,661	248,579	146,966	41,026	27,479
1939	2,122,049	1,258,964	311,517	101,561	111,372	37,800	34,980
1940	1,826,821	1,092,188	355,902	78,927	51,155	14,229	19,237
1941	3,200,419	1,661,424	445,257	184,403	48,156	24,057	17,688
1942	1,082,821	1,915,201	768,475	211,553	80,392	14,838	5,620
1943	605,282	1,045,881	1,246,173	431,457	150,441	45,036	15,396
1944	1,280,902	769,230	651,701	665,170	241,392	74,172	19,884
1945	934,148	867,355	487,782	236,181	146,821	54,792	19,207
1946	532,707	377,911	145,670	57,557	35,734	23,978	6,531
1947	343,786	188,164	105,037	60,424	19,233	13,011	11,212
1948	869,469	187,954	68,105	24,252	8,349	3,760	7,786
1949	1,436,543	779,609	229,033	112,736	13,042	1,122	3,107
1950	1,129,439	996,899	391,172	74,493	15,767	365	79
1951	69,919	780,969	180,297	62,677	14,805	2,599	278
1952	5,212	23,066	56,452	13,515	3,693	428	–
1953	6,769	39,824	11,747	50,186	4,294	807	144
1954	204,733	230,795	73,542	44,331	64,279	5,986	–
1955	72,158	269,874	141,748	25,484	10,665	20,547	1,078
1956	20,631	92,550	118,962	28,542	3,771	1,276	9,041
1957	60,212	80,371	35,949	33,731	6,459	991	606
1958	893,313	265,419	51,652	20,800	9,006	1,308	202
1959	313,017	220,673	31,168	1,953	626	132	427
1960	163,335	221,165	67,446	6,114	239	93	–

Schaefer (1954) and Widrig (1954). The most recent series of virtual population estimates is MacGregor's (1964). His estimates are compared with their equivalents from my analysis in figure 5. From 1935 ff., the general trends are the same and the theoretical objections to the virtual population (p. 8), already discussed, easily account for the discrepancies. The especially serious disagreement for the period 1932–1934 is associated with a rapid increase in fishing effort (table 11). It appears that in this instance the virtual population is inappropriate as an estimate of spawning stock size. It is similarly inappropriate for estimating year class size.

A method developed by Clark, in Clark and Marr (1955), overcomes part of the bias in the virtual population estimates. It involves taking an

TABLE 14. *Population table 1932–1960 based on total catches, table 13, the* E *values from tables 11 and 12, and formulas 16 and 17. Numbers above the step line are based on* M = *0.4 and table 11, those below on table 12 and* M = *0.8.*

Year	*Millions at Age Indicated*							*Total*	*Less ½ Two's*
	2	*3*	*4*	*5*	*6*	*7*	*8 and Over*		
1932	3,981	7,195	6,764	2,624	1,161	512	941	23,178	21,187
1933	8,680	2,570	3,162	3,240	2,181	1,025	2,496	23,354	19,014
1934	14,202	5,510	2,331	1,490	1,608	952	1,379	27,472	20,371
1935	4,098	8,808	2,748	991	1,171	493	766	19,075	17,026
1936	2,821	2,286	4,479	1,918	374	205	101	10,773	10,773
1937	5,383	1,515	1,719	1,127	295	151	54	10,244	10,244
1938	6,940	2,411	504	581	343	96	64	10,939	7,469
1939	6,763	2,762	683	223	244	83	77	10,835	7,453
1940	11,808	2,834	923	205	133	37	50	15,990	10,086
1941	14,442	6,440	1,725	715	187	93	69	23,671	16,450
1942	6,152	7,104	2,850	785	298	55	21	17,265	14,189
1943	3,268	3,251	3,872	1,341	467	140	48	12,387	10,753
1944	3,720	1,703	1,442	1,472	534	164	44	9,079	7,219
1945	2,620	1,470	826	400	249	93	33	5,691	4,381
1946	1,680	1,010	389	154	96	64	17	3,410	2,570
1947	2,349	700	390	225	71	48	42	3,825	2,650
1948	3,102	1,297	470	167	58	26	54	5,174	3,623
1949	4,921	2,008	590	290	34	3	8	7,854	5,393
1950	4,151	2,147	843	160	34	1	–	7,336	5,260
1951	2,205	1,876	433	151	36	6	1	4,708	3,605
1952	2,494	945	638	153	42	5	–	4,277	3,030
1953	3,380	1,118	414	455	39	7	1	5,414	3,724
1954	3,011	1,518	484	292	268	25	–	5,598	4,092
1955	935	1,221	641	115	48	135	7	3,102	2,634
1956	695	373	479	115	15	5	94	1,776	1,428
1957	1,216	299	134	125	24	4	2	1,804	1,196
1958	2,490	507	99	40	17	3	–	3,156	1,911
1959	1,327	561	79	5	2	–	–	975	1,311
1960	–	397	121	11	–	–	–	–	–

assumed or estimated coefficient of natural mortality and reconstructing the minimum population that must have existed at each year to yield the catches of that and subsequent years. One of her trials involved an estimated natural mortality rate of 0.51, close to the 0.40 used by me. While her results (1941–1950) are minimum estimates and are not free of the bias associated with changing fishing mortality, they are in much closer agreement with mine (fig. 6), than the uncorrected virtual population estimates.

In summary, the population estimates given in table 14 result from computations based on an analytical framework that is more nearly correct than those previously applied. Most of the information available on the

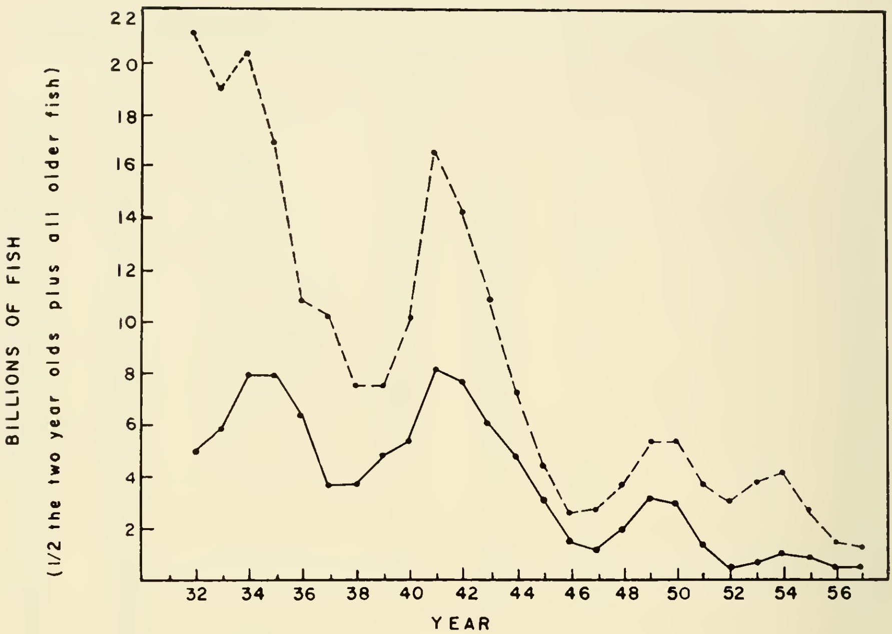

FIGURE 5. Comparison of estimated spawning populations (table 14) with virtual populations from MacGregor (1964). Dashed line from table 14. Solid line from MacGregor (1964), table 1.

sardine has been incorporated in the calculations, and the results are entirely consonant with all available information that was not formally incorporated. As such, these estimates provide an improved basis for examining the history of the population.

Biomass Solution

Although most workers have treated the sardine population in terms of numbers, the biomass of the population is of greater interest, both biologically and with respect to fishery problems. Numbers could be converted to biomass for each age-group and then the age-groups totaled. A more direct way, employed here, is to obtain an estimate of the total biomass of the older fish by subtracting the weight contribution of the fish less than 3 years old from the weight of the total catch, and dividing the difference by the fraction of the population caught (E). The biomass of the 2-year-olds was computed separately by multiplying the population numbers by the estimated average weight. This was then added to the weight of the older fish, the sum being the total weight of the population of fish 2 years and older.

For this purpose, adequate data on the relationship between length and

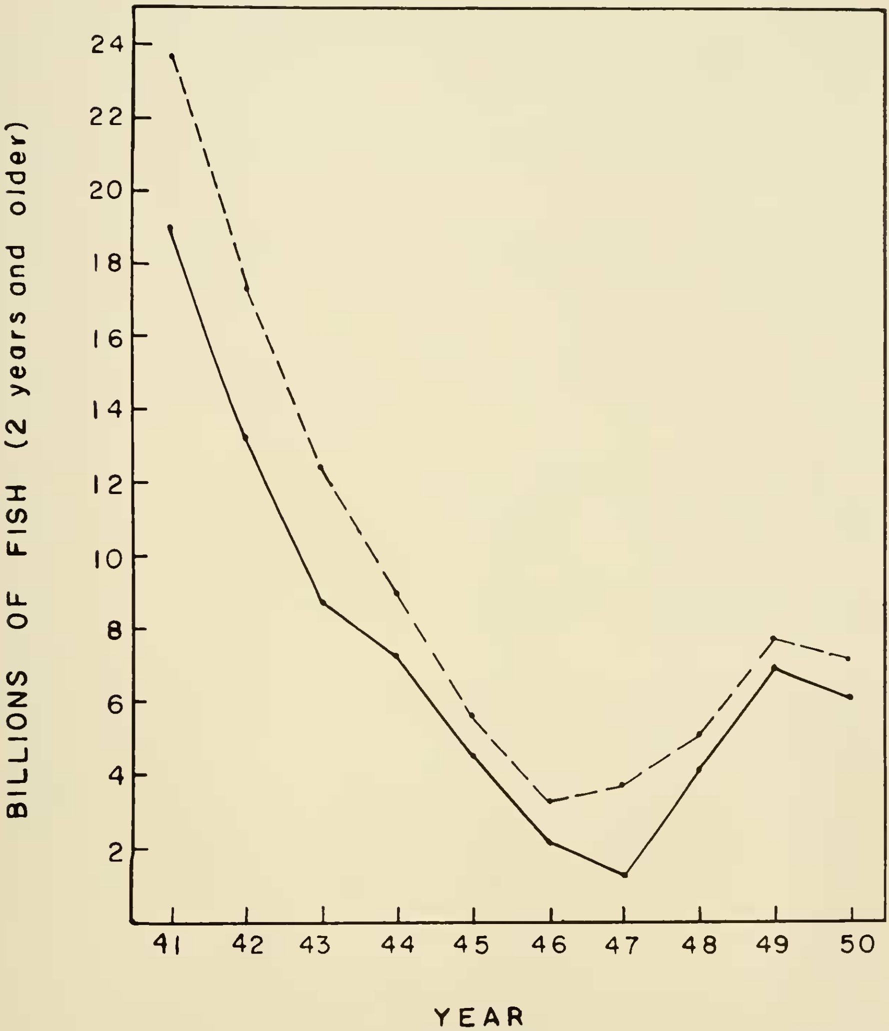

Figure 6. Comparison of population estimates (table 14) with corrected virtual population estimates computed by Clark (in Clark and Marr, 1955, table 12). Dashed line from table 14. Solid line from Clark.

age are available from 1941 onward: Phillips (1948), Felin and Phillips (1948), a series of papers keyed in Wolf (1961), and Wolf and Daugherty (1963). These were transformed into weights using the relationship developed by Clark (1928), a relationship apparently still valid (John MacGregor, personal communication). For the earlier period, 1932–1940, the mean values for 1941–1946 were used. In order to test the validity of this extrapolation,

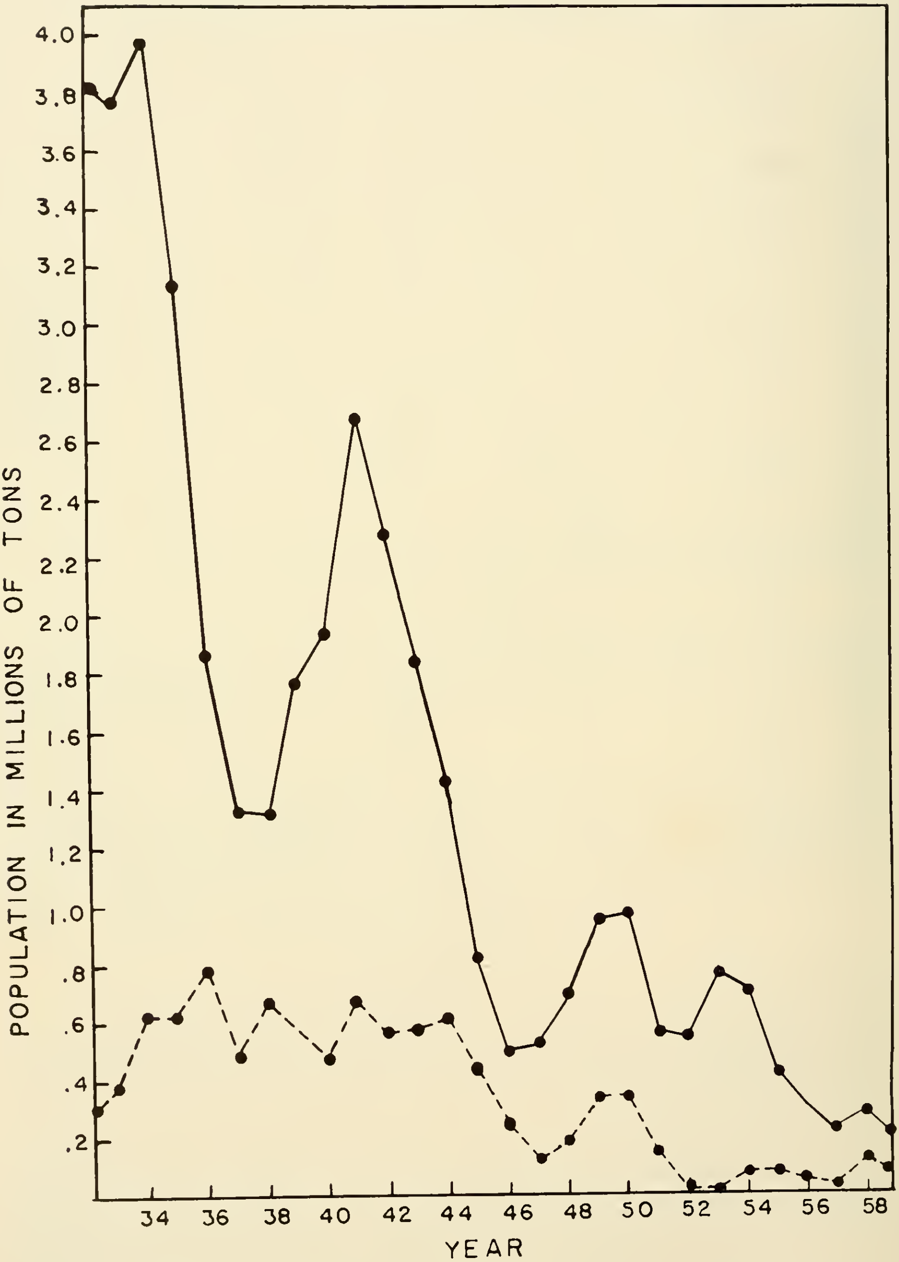

Figure 7. Estimated biomass of sardines 2 years and older, and landings, 1932–1959. Biomass—solid line, landings—dashed line.

the weight of the catches was reconstituted from the numbers and age for each year, and compared with the true or measured total weight. The maximum discrepancy was 17 per cent, with the majority agreeing well within 10 per cent. In the calculations done here this error range is, of course, considerably reduced because the only reconstituted weights used were for the younger (0-, 1-, and 2-year-old) fish, and zeros and ones form an insignificant fraction of the catch.

The biomass estimates derived by this procedure are given in table 15 and presented graphically in figure 7. They show a rapidly declining population with relatively short-lived reversals representing the passage of one or more abundant year classes through the population, *e.g.*, the 1938 and 1939 year classes were the principal components of the peak in 1940–1943. The landings of the fishery show a similar trend (fig. 7), although there are considerable differences in detail. The major discrepancy appears during the early years when the fishery was removing a much smaller fraction of the total population and was apparently fishing down a large "virginal" stock. Comparison of tables 14 and 15 readily points up the bias involved if numbers are used as a basis for measuring the population. For instance, on the basis of biomass, the 1932 population was 5.8 times the 1954 population, but on the basis of numbers it was only 4.1 times.

RELATION BETWEEN SPAWNING BIOMASS AND REPRODUCTION

Up to this point we have been concerned with developing a method of estimating population numbers from the catch and other statistics. The method has been applied and the results have been expressed in terms of numbers and biomass. This information can now be examined with respect to population regulation.

Potential Reproduction in the Absence of a Fishery

In any steady state population one egg must eventually result in one egg. The eggs produced in any one year can be estimated if an estimate of spawning age fish is available, and the relation between eggs and spawners is known. Numbers of spawners cannot be used because the age structure of the population is constantly changing. MacGregor (1957) has, moreover, shown that fecundity is nearly proportional to biomass. I will, therefore, use the calculated biomass of the population as estimates of yearly egg production.

Reports by Clark (1934) and MacGregor (1957) suggest that during the early years of the fishery about half of the 2-year-olds matured and spawned. Information on the population during the late 1950's (Ahlstrom, 1960) shows that all of the 2-year-olds spawned. The most logical time to introduce the transition is 1951 when the 1949 year class, the first to be characterized as

TABLE 15. *Estimated biomass of Pacific sardine population 1932–1959. Includes all fish 2 years and older.*

Year	Thousands of Tons	Year	Thousands of Tons
1932	3,884	1946	506
1933	3,764	1947	524
1934	3,996	1948	687
1935	3,136	1949	958
1936	1,861	1950	973
1937	1,330	1951	570
1938	1,324	1952	554
1939	1,772	1953	709
1940	1,940	1954	668
1941	2,709	1955	425
1942	2,276	1956	293
1943	1,849	1957	212
1944	1,389	1958	281
1945	835	1959	190

dominantly southern race, became 2-year-olds. The series will, therefore, be divided into two segments for examination, *i.e.,* 1932–1948 and 1949–1957, employing 1951 as the first spawning year during which all 2-year-olds are presumed to have spawned. The estimates developed previously are, strictly speaking, for populations in existence at the beginning of the fishing season, about September 1. Maximum spawning occurs about 5 months earlier. During these 5 months, the sardine population is subject to natural mortality but the fish are also growing, so I have assumed that the two processes are in approximate balance, and that any remaining bias is small and probably has an equal effect on the measure of year class size.

Because the sardine spawns over a considerable number of years, it is not possible to use the uncorrected number or biomass of a single age-class to estimate the total number of eggs eventually produced by the fish resulting from one year's spawning. The procedure adopted (tables 16 and 17) was to estimate the spawning biomass of 2-year-old fish over their entire spawning life relative to their biomass at age 2. The schedule is based on the estimated natural mortality and the known relation between age, length, and biomass. The estimated biomass of 2-year-olds in any one year multiplied by the factor computed in this way provides an estimate of the eggs that would be produced by this year class in the absence of fishing mortality, in the same terms as the estimate of eggs produced in one year. I have termed the measure of year class strength "reproductive potential biomass," or more succinctly, "reproductive potential." The principal problem with respect to the computations in tables 16 and 17 was obtaining an accurate and representative estimate of growth.

Table 16. *Computation of factor to relate biomass at age two to "potential spawning biomass," 1932–1948 year classes. Growth data from Phillips (1948, table 9).* M = *0.40.*

Age	*Number*	*Length*	*Estimated Growth Weight*	*Biomass*
2	1,000	197	93	93,000
3	670	217	123	82,410
4	449	231	152	68,248
5	301	240	170	51,170
6	202	246	183	36,966
7	135	250	193	26,055
8	91	253	202	18,382
9	61	255	205	12,505
10	41	–	205	8,405
11	27	–	205	5,535
12	18	–	205	3,690
13	12	–	205	2,460

Σ less half 2's = 362,326; 362,326 ÷ 93,000 = 3.896 = factor.

The growth estimates used for the period 1932–1950 were based on adequate sampling over a number of years, but data for the recent period are less adequate, particularly the samples from Mexico. However, during 1958–1960, the population was farther north and, thus, was more adequately sampled in California, while an improved system of sampling the Mexican landings was in operation. Weighted mean lengths for each age were computed for the season catches of each of these 3 years (Wolf and Daugherty, 1961; Gates and Wolf, 1962; Wolf and Daugherty, 1963) and from these, unweighted mean values for the 3-year period were obtained. The results for ages 2 to 6 formed a straight line when plotted as length at age n against length at age $n + 1$. The observed length at age 7, for which only a few measurements were available, did not fall on the line, so the extrapolated value was employed.

As pointed out above, the calculated "biomass of parents" (P) and "reproductive potential" (R) in terms of biomass (table 18) are nearly proportional to the biomass, or numbers of eggs spawned. The data are treated in two parts because of the change in population parameters (growth and natural mortality) beginning with the 1949 year class. Figures 9 and 10 are plots of reproductive potential as a function of the biomass of parents, together with an equilibrium line and the reproduction function developed by Ricker (1954), fitted as outlined in Ricker (1958a), and illustrated for one of the periods in figure 11. The equilibrium line represents the steady state situation. Any population for which the points fall consistently below this line is heading for extinction; conversely, any that plots only above it would increase without limit. A perfect fit to the 45° line is highly improbable. In

TABLE 17. *Computation of factor to relate biomass at age two to "potential spawning biomass," 1949 to 1957 year classes. Growth data estimated from unweighted mean lengths of season landings, 1958–1960.* M = 0.80.

Age	Number	Length	Estimated Growth Weight	Biomass
2	1,000	193	86	86,000
3	449	203	103	46,247
4	202	214	120	24,240
5	91	223	137	12,467
6	41	230	150	6,150
7	18	236	162	2,916

$\Sigma = 178{,}020$; $178{,}020 \div 86{,}000 = 2.07 =$ factor.

order to maintain a steady state there must, then, be a compensatory mechanism that tends to reduce population growth at high densities and accelerate it at low densities, so that, on the average, the points are approximately equally distributed on both sides of the line.

The data in figures 9 and 10 are much too variable to form the basis for developing a reproduction function; indeed, it is doubtful if any function would reduce the variance significantly below that associated with the mean of the year class measure. Therefore, reduction of variance offers little or no guidance in selecting a reproduction function. A function, if it is to be chosen at all, must be selected on the basis of other criteria.

Two functions have been advanced to relate spawning success to adult stock (Beverton and Holt, 1957; Ricker, 1954), both of which assume compensation in the preadult stages. The Beverton and Holt model is asymptotic to a horizontal line representing the maximum number of progeny. This does not seem attractive in the present instance because recruitment at the higher population levels seems to fall off. Apart from this objection, fitting the Beverton and Holt function to the data results in an estimated maximum population of 1.8×10^6 tons for the 1932–1948 period, which seems too low and yields very high values of the year class measure (R) at low stock densities. The variance about this curve is much larger than that around the mean of R. The variance about the Ricker function, which will be considered in greater detail, is only 8 per cent higher than that associated with the mean.

Ricker (1954) published a general study of adult stock and reproduction relationships. He was particularly interested in cases where, on the basis of biological information, it appeared that compensation took place in the preadult stages. This is thought to be true of the sardine. His equation is:

(19) $$R = Pe^{(P_r - P)/P_m}$$ (Ricker, 1958a)

FIGURE 8. Size of year class as numbers at age 2 when they are first recruited to the fishery versus the year spawned.

where: $R =$ Reproduction,
$P =$ Parental or spawning stock,
$P_r =$ Stock size at which $R = P$,
$P_m =$ Stock size giving maximum reproduction in the absolute sense.

The relationship has several attractive features. The ratio, R/P, increases as P approaches zero. The maximum reproduction in the absolute sense may be anywhere on the P axis, depending on the distribution of the observed values. A functional mechanism that might underlie his model is cannibalism. Unlike the plaice considered by Beverton and Holt (1957) where the adults

TABLE 18. *Biomass of parents* (P) *and reproductive potential* (R) *of year classes 1932 through 1957.*

Year	Thousands of Tons	
	Spawning (P)	Year Class (R)
1932	3,627	6,039
1933	3,291	1,743
1934	3,221	1,200
1935	2,912	2,289
1936	1,707	2,951
1937	1,036	2,876
1938	946	5,021
1939	1,032	5,521
1940	1,296	2,563
1941	2,001	1,334
1942	1,947	1,678
1943	1,678	1,182
1944	1,174	758
1945	684	1,039
1946	409	1,266
1947	391	2,135
1948	525	1,997
1949	684	503
1950	716	636
1951	570	787
1952	554	674
1953	709	228
1954	668	221
1955	425	255
1956	293	375
1957	211	260

are benthic and the larvae are pelagic, the sardine adults and the eggs and larvae inhabit the same area. Further, Hand and Berner (1959) show that fish eggs occurred in 79 per cent of their sample of 273 sardine stomachs and larvae in 17 per cent. They report, "We found very few sardine eggs in sardine stomachs." This contrasts with Davies' (1957) finding that the majority of fish eggs in the stomachs of South African sardines were of that same species. Thus, it appears that the Ricker equation offers a reasonable framework for consideration of the record in its entirety.

The equation involves two constants P_r and P_m. Both can be derived from the linear regression of $\log_e R/P$ on P. P_r is the value of P when $\log_e R/P$ equals zero. It takes account of the general environmental resistance, compensatory mortality, and the growth, fecundity, and mortality schedules of the adults. The quantity P_m is estimated as minus the reciprocal of the

slope of the regression. Its value relative to the value of P_r reflects the comparative effectiveness of compensatory and noncompensatory mechanisms. Its value is entirely dependent on compensatory mechanisms, *i.e.*, a steep slope is associated with a high degree of compensation and vice versa. When P_m is greater than P_r, noncompensatory mechanisms are more important; when P_m is smaller than P_r, the reverse is true. The implicit assumption is that these factors remain constant over the years under consideration. This was not true for the sardine data, which had to be considered in two segments.

One interesting question is whether the relationship between spawning stock and potential year class biomass in the years 1949–1957 (fig. 10) involves any new elements, or whether the difference from the 1932–1948 relationship (fig. 9) can be accounted for by the changes in growth and natural mortality already discussed. To test this, the weights at age *2* for the period 1949–1957 were adjusted upwards by a factor of 1.5 ($e^{0.4}$), on the assumption that the increased mortality in the third year of life ($M = 0.8$ versus 0.4 for the later period) implies proportionally greater mortality in the second year. These adjusted figures were then multiplied by the 1932–1948 potential biomass factor (table 16) to obtain an estimate of "potential" reproduction for the years 1949–1957, provided the natural mortality and growth parameters of the 1932–1948 period had prevailed. The new points when treated independently yielded a Ricker curve approximating the curve for the period 1932–1948. When these adjusted values and the data for 1932–1948 were pooled, the parameters of the 1932–1948 curve were changed less than 5 per cent. Thus, the postulated changes in growth and adult mortality appear to explain adequately the discontinuity between the two series.

The largest ratios of potential year class biomass to spawning stock biomass for the two periods were 5.35 in 1939 and 1.4 in 1951. These compare very well with the values predicted from the Ricker function as the stock approaches zero: 4.0 and 1.9. Thus, both the long empirical record and the fitted function indicate that the average resilience of the population is a great deal less than the 90 thousand eggs produced per female might suggest, and that really large year classes are not to be expected from small spawning stocks. The maximum ratios of 4 and 5.35 presumably represent general environmental resistance as well as compensatory mechanisms.

The considerable variability in potential year class biomass (7.9-fold variation in 1932–1948; 3.8-fold in 1949–1957) is quite in line with the numerous examples provided in Ricker (1958a) and Beverton and Holt (1957). For example, North Sea haddock range over 50-fold; British Columbia herring, 8-fold; and Tillamook Bay, Oregon, chum salmon, 10-fold. Such variation at any one spawning stock size, *e.g.*, the wide range in spawning success of the sardine at about one million tons of spawners (fig. 9), probably

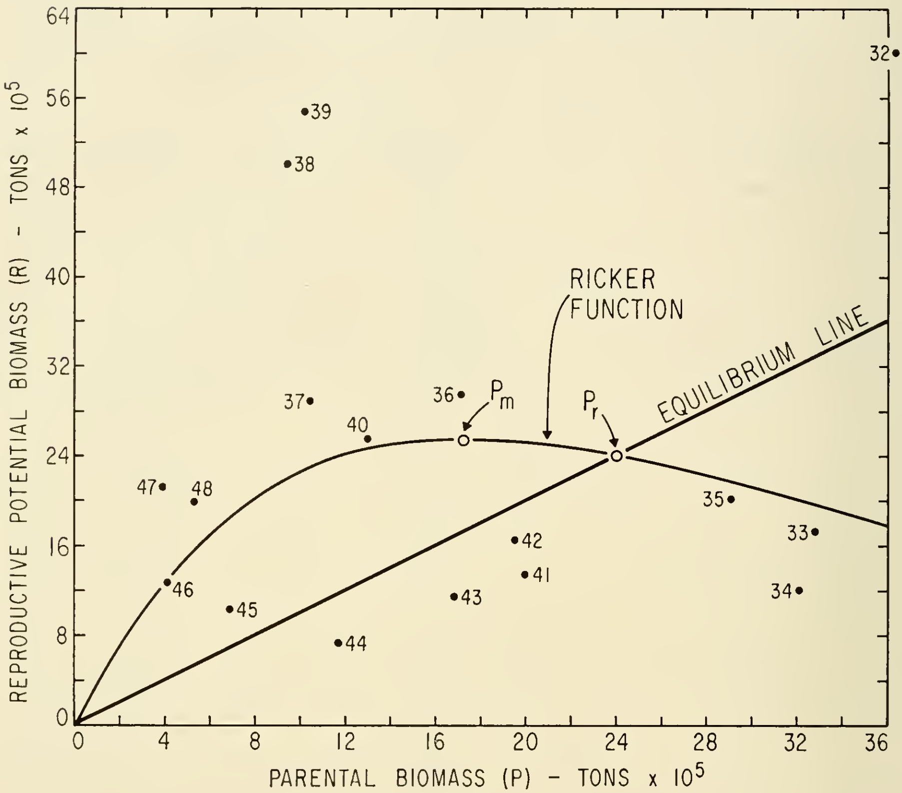

FIGURE 9. Relation between biomass of parents (P) and reproductive potential (R) of year class. The straight line represents replacement reproduction. The fitted Ricker reproduction function is also shown. Period 1932–1948. Numbers are calendar years. P_r, the equilibrium population, is 2,403,000 tons. P_m, the population giving the maximum absolute reproduction, is 1,729,000 tons.

reflects changes in the ocean environment. Determining the causes of these variations may not, however, be a tractable problem. For example, the least successful year in terms of R/P (1934) and the most successful year (1939), differ by a factor of 14.4. This difference could be induced by a coefficient of total mortality (Z) only 1.33 times as great in 1932 as in 1939, if we assume the difference in mortality occurred from egg to age 1 and was spread evenly over the first year, *i.e.*, that the instantaneous rate is the correct approach. Considering the sampling problem in the ocean, a 35 per cent change in some vital process would be exceedingly difficult to detect, even if we knew exactly what to try to sample! An alternate extreme hypothesis that should be easier to study because a continuously integrated process is not involved, is to propose that environmental conditions during some relatively brief and

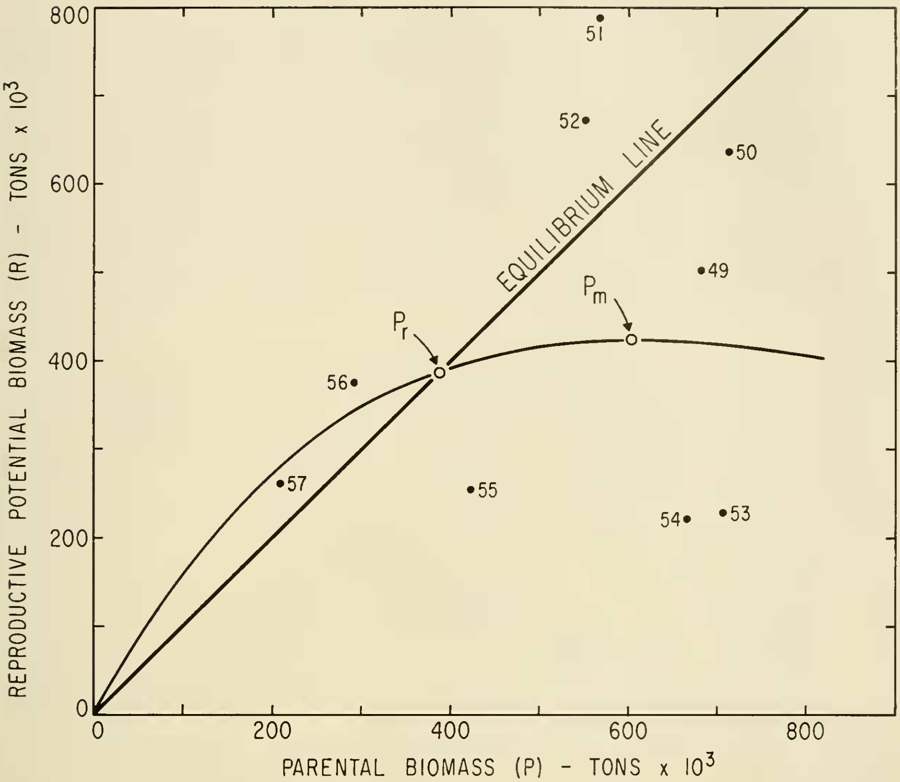

FIGURE 10. Relation between biomass of parents (P) and reproductive potential (R) of year class. The straight line represents replacement reproduction. The fitted Ricker reproduction function is also shown. Period 1949–1957. Numbers are calendar years. P_r, the equilibrium population, is 389,000 tons. P_m, the population giving the maximum absolute reproduction, is 602,000 tons.

critical period vary widely (for example, proposing that low survival is caused by a flow pattern that carries most of the eggs to unfavorable areas during some years, and vice versa). Such a model was elaborated for the sardine by Sette (1960). Marr (1960) discounted it on the basis that such evidence as was available (drift bottle records and oceanographic surveys) did not support it. At present, the hypothesis is still a moot question.

The values of the biomass of potential year classes are about evenly divided between those greater and those smaller than the spawning stock (figs. 9 and 10). They are not, however, randomly distributed in time in the years 1932–1948 (runs test, $p < 0.025$) but may be in the later period (runs test, $p \sim 0.25$). An analysis of the position of the points relative to the line of prediction of the Ricker curve gives similar results. The frequent occurrence of

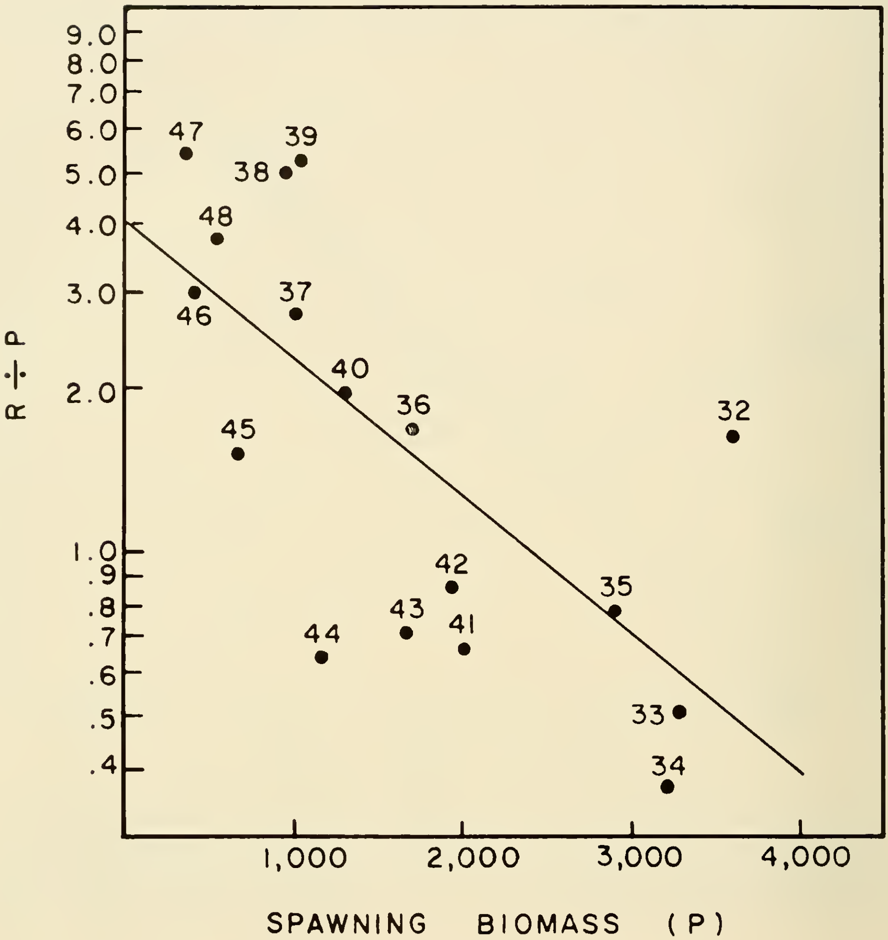

FIGURE 11. Least squares fit of the relation between P and ln R/P for the 1932 to 1948 year classes.

runs of 3 to 5 consecutive years with poor spawning success requires for population survival an age composition that will enable it to maintain itself in the face of several consecutive poor survival years. Though this problem will be considered in greater detail in a later section, it is worth noting here that one of the most obvious effects of a fishery is to reduce the span of ages contributing significantly to the population, thus amplifying the effect of environmental events on the population.

EFFECT OF THE FISHERY ON REPRODUCTION

The pertinent questions are whether the fishery is intense enough over

a period of time to reduce the spawning stock to a point where it can no longer be expected to yield a significant crop, and whether the intensity of fishing is high enough to keep the actual year class reproduction at or below the equilibrium line on the average. The data just discussed (figs. 9 and 10) show that by the criterion of "potential reproduction" the population would have had considerable resilience. For example, in the 1932–1948 period, after stock was reduced below P_r, *i.e.*, 2.4×10^6 tons, the sum of the plus deviations with reference to the equilibrium line was much larger than the sum of the minus deviations. The same is true for the 1949–1957 period, but the number of points is too small to permit any confidence in this observation.

The effect of the fishery is shown in figures 12 and 13. These are based on the population estimates (table 14) and the observed age–weight schedules. The biomass of spawners is the same but instead of potential year class biomass reproduction, actual reproduction is plotted on the y axis. The actual spawning biomass of each year class (actual year class biomass) was directly computed by summing the observed biomass of each year class as it passed through the population as opposed to the projections used to compute potential biomass. The difference between the two sets of figures (9 and 10 versus 12 and 13) represents the effect of the fishery. Under its influence, the sum of the negative deviations from the 45° line was markedly larger than that of the positive, agreeing with the observed decline of the population.

The cause of the marked change in the population in the 1949–1953 period can now be qualitatively explained. In the period 1945–1950 the spawning population was small (700,000 tons or less). As a result of the total mortality schedule (fishing and natural), 85 per cent of the biomass of the population was comprised of 2- and 3-year-olds during those years. If we now assume a failure of the reproduction of the northern race for two years (1949 and 1950), all of the 1949 and 1950 year classes would have been southern fish. This argument is similar to that advanced by others, *e.g.*, Marr (1960) and Sette (1960), but it was not considered by them in the context of a reduced, heavily fished population made up of only a few ages. By 1952, when these year classes were the two's and three's, the total tonnage of 4-year-olds and older was only 126,000 tons. If the fraction that was the northern race can be regarded as proportional to that in earlier years, about half of these would have been northern stock and this race which was once dominant now would be reduced to only 60,000 tons. Therefore, the parameters of the population as a whole would be changed from those appropriate for the northern race to those for the southern race. This argument may be overdrawn, but other events have operated in the same direction. For example, availability in 1947 and 1948, and 1952 and 1953, was generally low, so that the fishery, still centered off southern California and northern Baja California, must have

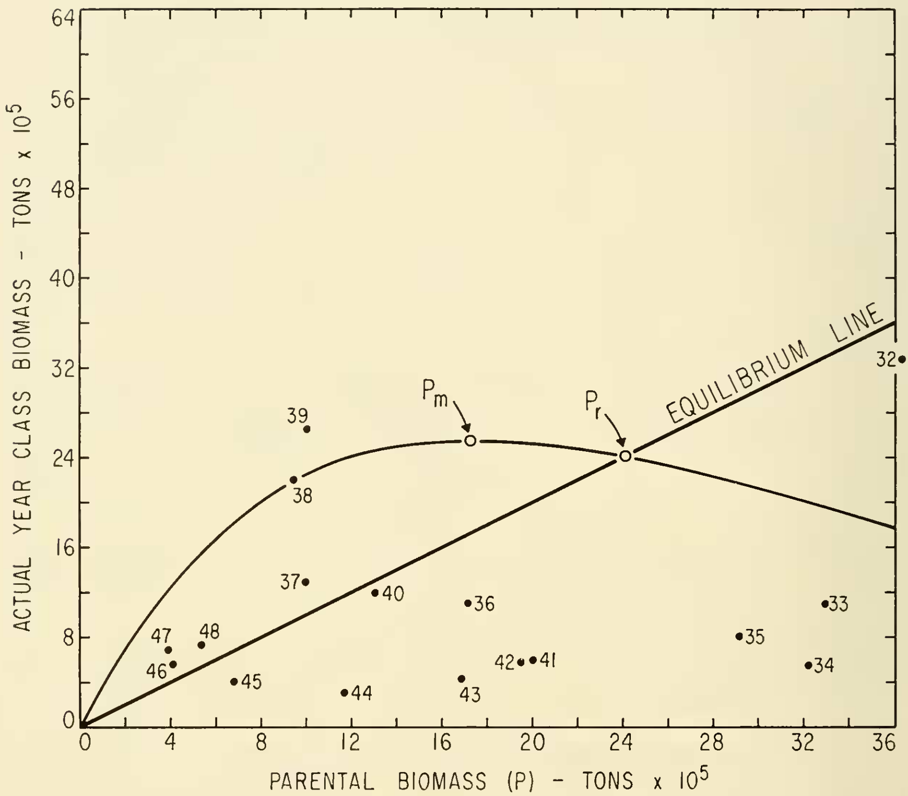

Figure 12. Relation between spawning biomass and actual year class biomass. Period 1932–1948. Numbers are years.

drawn principally from the remnant northern stock (Vrooman, 1964), thus depressing it far more than would have occurred if the sardines as a whole had had a more northerly distribution. It is not certain that fishing mortality was the cause of the change in the population structure, but in 1932, only 39 per cent of the biomass of the older fish was comprised of 2- and 3-year-olds. Clearly the effect of the 1949 and 1950 events would have been less had there been more older fish in the population. These aspects of the sardines' biology will be considered again in the discussion of practical problems.

BIOLOGICAL EFFECTS OF THE DECLINE OF THE SARDINE

In general it would be expected that a marked reduction of a particular species would be followed by readjustment of the populations of other species in the community. Whether or not this readjustment would be readily detectable might depend on several factors, but certainly prominent among these

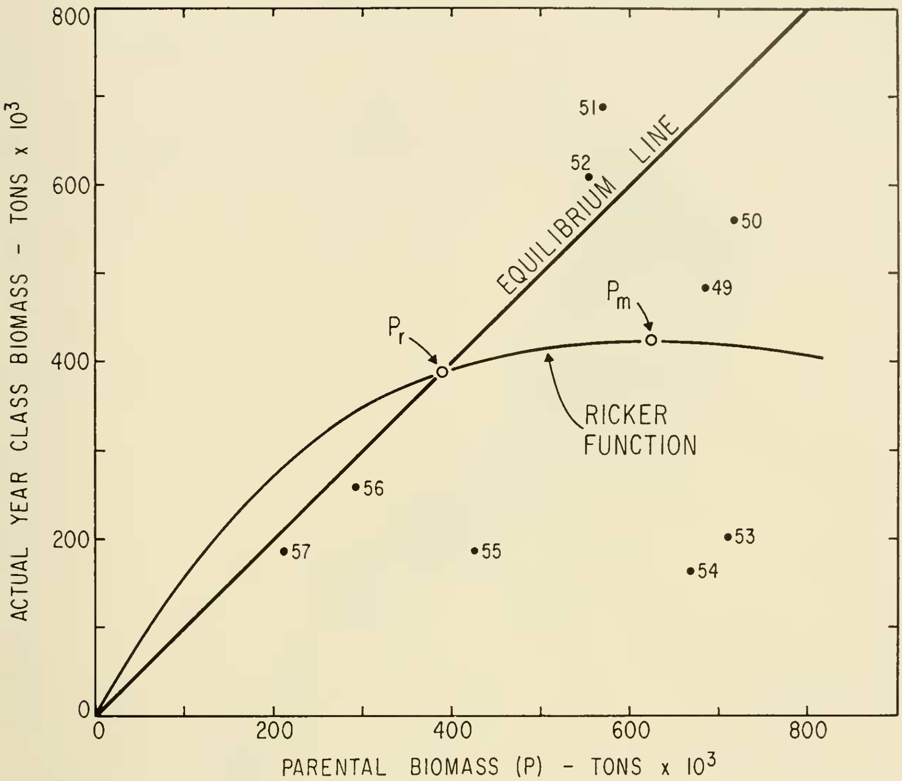

Figure 13. Relation between spawning biomass and actual year class spawning biomass. Period 1949–1957. Numbers are years.

is whether the species that was reduced was a major component of its community. The simplest way to evaluate this aspect of the problem is to explore the significance of the sardine's food requirements relative to the amount available to the entire trophic level.

The Food Supply of the Sardine Habitat

As will be at once apparent, the food supply in the habitat of the sardine is not known with precision. In fact, there is no real basis for more than very approximate arguments. On the basis of some simple considerations, however, it appears that the sardine population was an important element in the economy. Further, there is some basis for assuming the existence of competition for food within the California Current area.

The standing crop of zooplankton in the California Current region has been examined in some detail. (See, for example, Thrailkill, 1956.) For the purposes of this discussion I will use the results of the 1952 survey as a representative

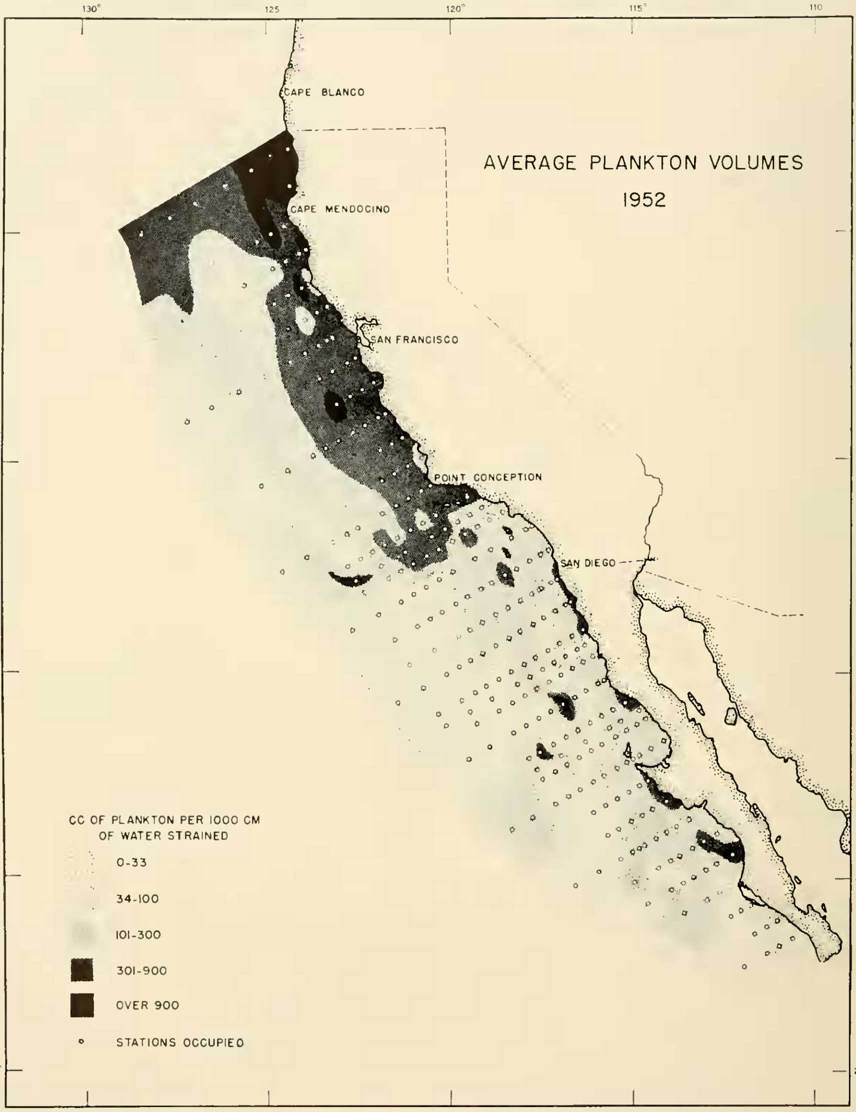

FIGURE 14. Average plankton volume for 1952 from Thrailkill, 1956, expressed as cubic centimeters of plankton per thousand cubic meters of water.

example (fig. 14). The area covered is about 1,200 miles long, roughly the north–south range of the sardine population if the seasonal migration of a fraction of the population to the Pacific Northwest is discounted. The sardine is known, from the egg surveys, to range in numbers up to about 200 miles

offshore. Thus, we are concerned with 24×10^4 square miles, or about 70×10^{10} square meters.

The depth of the plankton sampling was about 150 meters, established on the basis of the depth distribution of the sardine. Parenthetically, it might be pointed out that this is roughly the depth zone in which the bulk of the zooplankton occur. The average concentration of zooplankton in 1952 was 0.2 gram per cubic meter. This value, summed over area and depth results in an estimated standing crop of 21×10^{12} grams wet weight of zooplankton. At 1,000 calories per gram wet weight this standing crop represents 21×10^{15} calories.

Dr. Reuben Lasker (personal communication) has determined that adult sardines consume about 2 small calories per gram per hour.[2] The annual standing crop of fish 2 years old and older was estimated at about 4×10^6 tons for the period 1932–1934. The respiration requirement of this population was then 70×10^{15} calories per year. If the population was in a steady state, the loss of fish was balanced by growth. The annual loss at $M = 0.4$ would be 1.196×10^{12} grams. Based on determinations by Lasker of about 2,000 calories per gram wet weight, this would be equivalent to 2.4×10^{15} calories. Thus, the total caloric requirement was 72.4×10^{15}.

Sardines feed mostly on zooplankton (Hand and Berner, 1959). On this basis it would require about 3.5 standing crops of zooplankton to meet the energy requirements of the sardines. One possible source of additional food is advection. That there is more zooplankton coming in than going out is indicated by figure 13, where it is shown that the southward-flowing waters off California are a region of net consumption of zooplankton, an observation previously made by Reid (1962). An estimate of the annual rate of flow based on $1.5 \times 10^6\ m^3\ sec^{-1}$ across a line extending seaward from Point Conception between the surface and 150 meters (Reid, personal communication) is $47 \times 10^{12}\ m^3$ per year. If the inflowing water is estimated to contain about 0.6 gram of zooplankton per m^3 and the outflow, 0.05, the net contribution of advection is 25.9×10^{15} calories per year at 1,000 calories per gram wet weight of zooplankton, or about one standing crop. Thus, the sardines alone would require about 2.5 *in situ*-produced standing crops per year, in addition to the contribution of advection, for their maintenance. An obvious difficulty with the basic estimates of zooplankton is that they include unknown proportions of low-calorie organisms such as small salps. A source of error in the opposite direction is the unknown quantity of zooplankton not sampled and undersampling during the day. Finally, the turnover rate of zooplankton in the California Current area is not known, but it seems likely that it is no greater than five times per year.

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[2] This figure may be about 30 per cent high as Lasker's specimens had a lower fat content than typical fish in nature.

Table 19. *Summary record of anchovy and sardine larvae captured each year and sardine spawning biomass from table 18.*

Year	Numbers		Anchovy / Sardine	Sardine Spawning Biomass
	Sardine	Anchovy		
1951	11,066	29,552	2.7	570
1952	24,559	63,057	2.6	554
1953	15,055	103,928	6.9	709
1954	26,914	161,254	6.2	668
1955	14,121	140,183	9.9	425
1956	15,523	134,931	8.7	293
1957	9,833	146,631	14.9	212
1958	11,423	205,457	18.0	281
1959	5,308	206,000	38.8	190

Although the numbers are highly imprecise, they strongly suggest that the reduction of the sardine population to one-tenth of its former abundance was an event of first-order importance in the biological economy of the California Current region, and that the energy made available by the decline of the sardine should be reflected in an increase in other elements of the community of organisms in the area. Further, the apparently large share of the annual total required by the sardine alone and the smaller amount of plankton leaving the system than coming in raise the possibility of "competition" for food.

The Rise of the Anchovy (*Engraulis mordax* Girard)

In this section, I want briefly to consider the most obvious biological event associated with the decline of the sardine. The record, in summary, appears in table 19. The recent surveys show anchovy larvae are by far the most abundant of all fish larvae; in fact, the numbers captured, despite escape of the very small larvae, are about equal to the numbers of all other species combined (*cf.*, Ahlstrom, 1959b), and about three times the numbers of all other plankton-feeding fish combined.

Anchovies are about twice as fecund per spawning per unit weight as sardines (John MacGregor, unpublished data.) This is, however, nearly counterbalanced by undersampling of anchovy larvae by a factor of about 2 relative to sardines, *i.e.*, they tend to pass through the mesh of the net to a marked extent. Their protracted spawning season (see, *e.g.*, Ahlstrom, 1959b) suggests that they spawn as often per year as the sardine. Therefore, at first approximation and within the limits of sampling error, the numbers of larvae in table 19 can be considered proportional to the biomasses of the respective spawning populations.

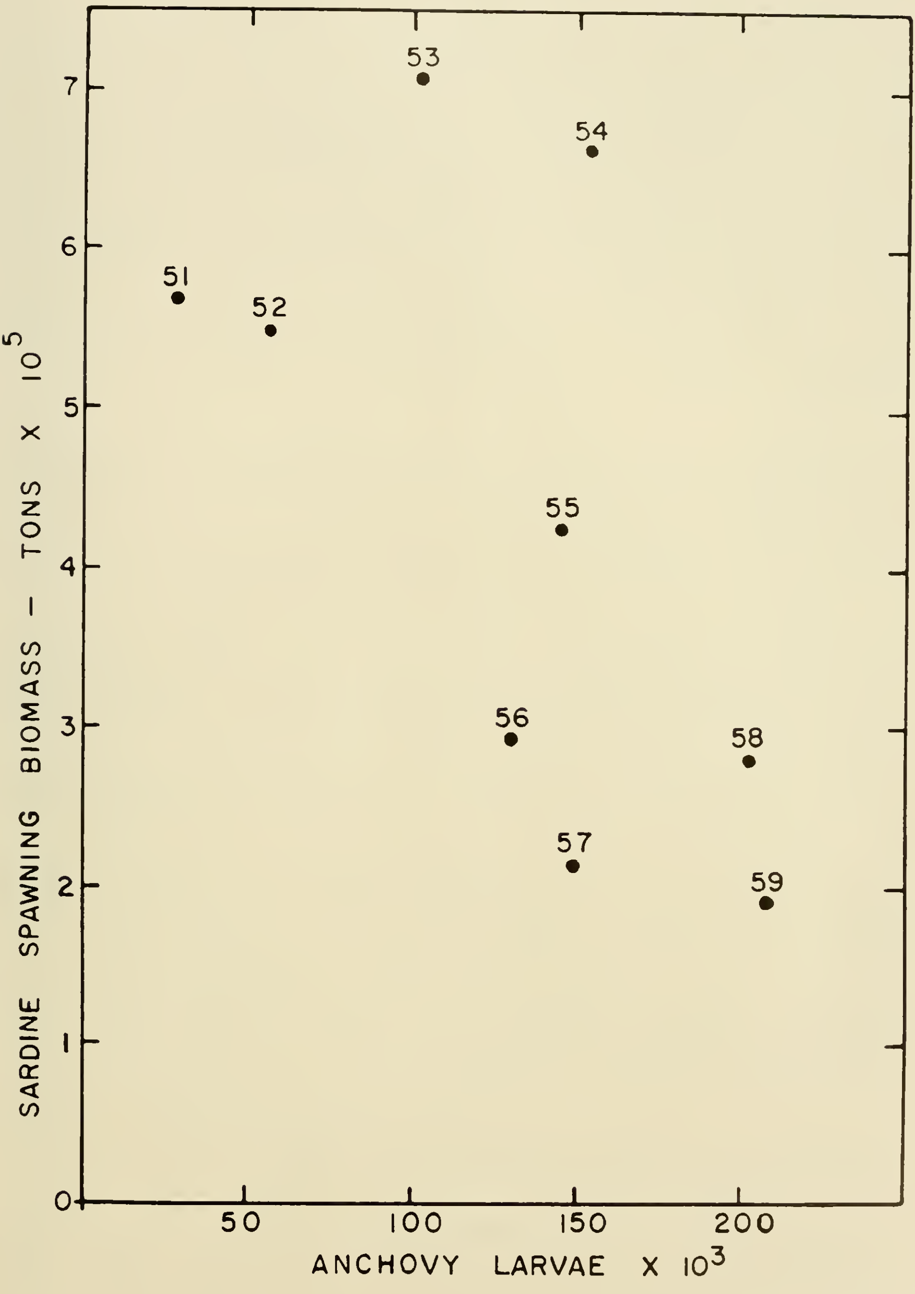

FIGURE 15. Sardine spawning biomass as a function of anchovy spawning biomass, as measured by the numbers of anchovy larvae taken. Sardine biomass from table 19.

The data in table 19 show the anchovy has risen and the sardine has declined during the period. This is also suggested by a plot of anchovy larvae and sardine spawning biomass, figure 15. The situation prior to 1951 is not known with certainty, but plankton samples taken during 1940 and 1941 (Ahlstrom, 1948) in the region between Point Conception and San Diego contained about the same numbers of anchovy and sardine larvae. However, as this survey involved only a segment of the total area, the estimated relative abundances cannot be determined as precisely as would be possible if the surveys had been as complete as they are now. What appears to be a reasonable extrapolation based on spawning distribution and trends in the 1950's suggests that, in terms of biomass, anchovies were then about half as abundant as sardines. They now (1957–1959) appear to be about 20–40 times as abundant.

If one pools the larval data (table 19) for the years 1957–1959, the ratio of anchovies to sardines is 21 : 1. Multiplying the average spawning population of sardines for the same period (table 18) by this factor yields an estimated anchovy spawning population of 4.8 million tons—rather close to the estimate at four million tons for the "primitive" sardine population in 1932–1934. Clearly, one can argue the details of this discussion, but the conclusion is inescapable that the anchovy, not the sardine, is now the important plankton-feeding fish in the California Current system, and that its present population level is close to that of the "primitive" sardine population. Moreover, Lasker (personal communication) finds they respire at the same rate as the sardine.

Similar considerations, primarily based on the information in table 19, have led several workers, *e.g.*, Murphy, 1961; Ahlstrom, 1960; Marr, 1960; and Isaacs, in press; to consider whether the rise of the anchovy can be causally related to the decline of the sardine. The possibility is attractive because the two seem to occupy overlapping niches. For example, the lower threshold temperatures for spawning are 11° C. for anchovies and 13° C. for sardines and the corresponding upper limits for significant spawning are about 20° C. for both (Ahlstrom, 1954, 1959a). Food habits of the larvae are similar (Arthur, 1956; Berner, 1959). Hand and Berner (1959) found Crustacea were the dominant food (89 per cent) of the adult sardine. They also found, particularly in northern fish, more phytoplankton than might have been expected, as an adventitious addition to a zooplankton diet. There is no exact information on the food of the adult anchovy but the impressions of myself and others, based on animals in captivity and cursory field examinations, suggest that they eat about the same things as sardines. There is nothing in their buccal anatomy, gill rakers, teeth, etc., to suggest they feed at a lower trophic level, whereas the Peruvian anchovy which feeds largely on phytoplankton has longer gill rakers. Finally, eggs, larvae, and adults of both species frequently occur together in the same area.

Two hypothetical mechanisms can be advanced to explain the apparent replacement of the sardine by the anchovy:

1. Direct confrontation at some stage(s) in the life history, or
2. A sequence of events, mediated through the environment, that results in the particular numerical balance between the species.

Marr (1961) postulated direct competition among larvae for food, *i.e.,* direct confrontation. Isaacs (in press) has, indirectly, examined this hypothesis by studying the co-occurrence and mortality of larvae of the two species. His results indicate to me that the decline of the sardine is not associated with increasing co-occurrence of sardine and anchovy larvae. Though this information does not disprove direct confrontation, it does not support it.

It could be suggested that the two species might interact by consuming each other's young. That is, the same mechanism advanced to explain compensatory regulation of the sardine population could also act to restrict the general level of both populations considered together. This could then be carried one step further by postulating that under some environmental regimes anchovies might drive down sardines by preying more heavily on their larvae. Again, there is no disproof, though neither Isaacs' observations nor the argument to be considered next offer support.

Sardine year class strength is negatively correlated with numbers of anchovy larvae (fig. 16, $\tau = -0.67$, $p < 0.10$). This may be due, in part at least, to the decline of the sardine spawning stock, but there is no way to remove the effect from the record except by expressing the sardine year class as a fraction of the spawning stock. When this is done, there is no discernible systematic relationship between this fraction and the numbers of anchovy larvae.

There are, on the other hand, several lines of evidence that suggest there has been no direct interaction of sufficient intensity to bring about the decline of the sardine. In addition to the negative arguments just considered there is the observation discussed on page 51 that the observed reduction in the reproductive efficiency of the sardine during the period of the 1950's can be accounted for by changes in growth rate and changes in the natural mortality of the adults. These two changes in turn appear to be associated with the change in dominance from the northern to the southern race. This change is ascribable to the fishery.

An additional and perhaps a more compelling argument stems from consideration of the recent history of the two populations (fig. 17). This presentation suggests that the rise of the anchovy followed the decline of the sardine rather than preceding or accompanying the decline. For example, in 1951 and 1952 the sardine stock was half a million tons and the anchovy population is estimated at about one and one-half million tons. By 1956–1959 the sardine stock had only been reduced by another one-fourth million tons,

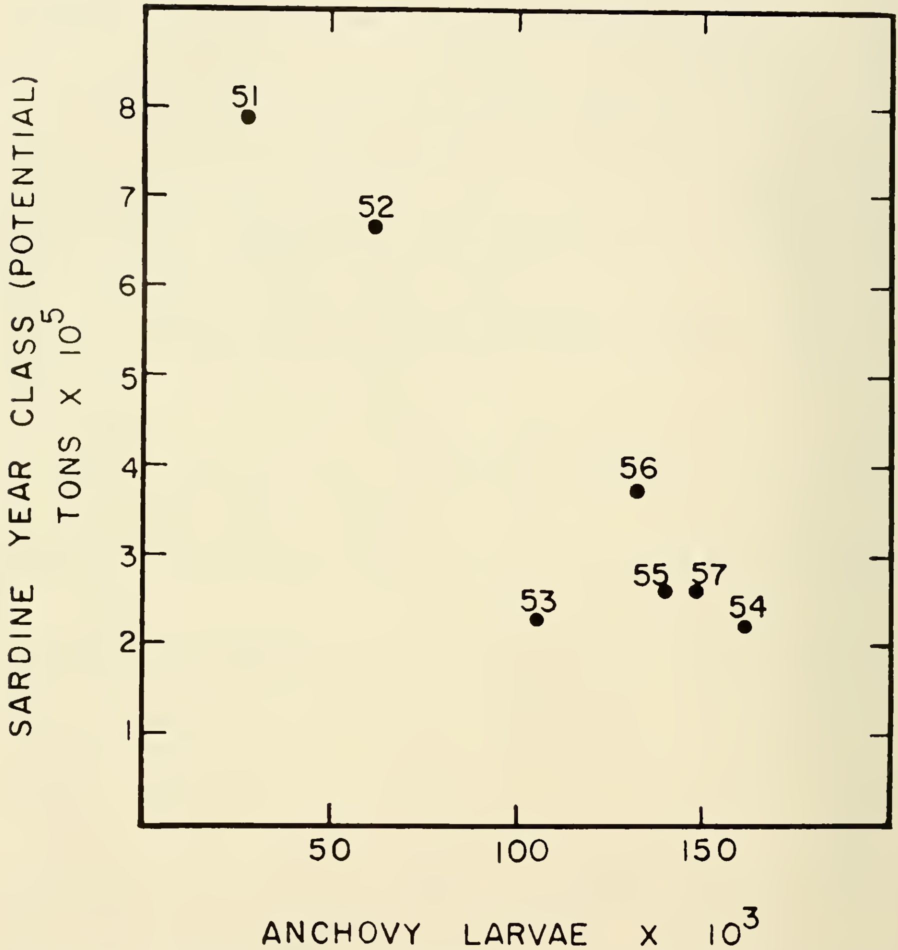

Figure 16. Sardine year class size (table 18) as a function of the biomass of spawning anchovies, as measured by the numbers of larvae taken.

but three million tons had been added to the anchovy population. Clearly, there was a time lag involved.

Nonetheless, it seems reasonable and consonant with the evidence to advance the hypothesis that the two species are fundamentally competitors. They occupy overlapping but not identical niches. Food seems to represent a major area of overlap, and the energy-food considerations developed earlier suggest food may be in short supply; and finally the size of the 1957–1959 anchovy population is about the same as the 1932 sardine population.

Even though it does not appear possible, at present, to identify the

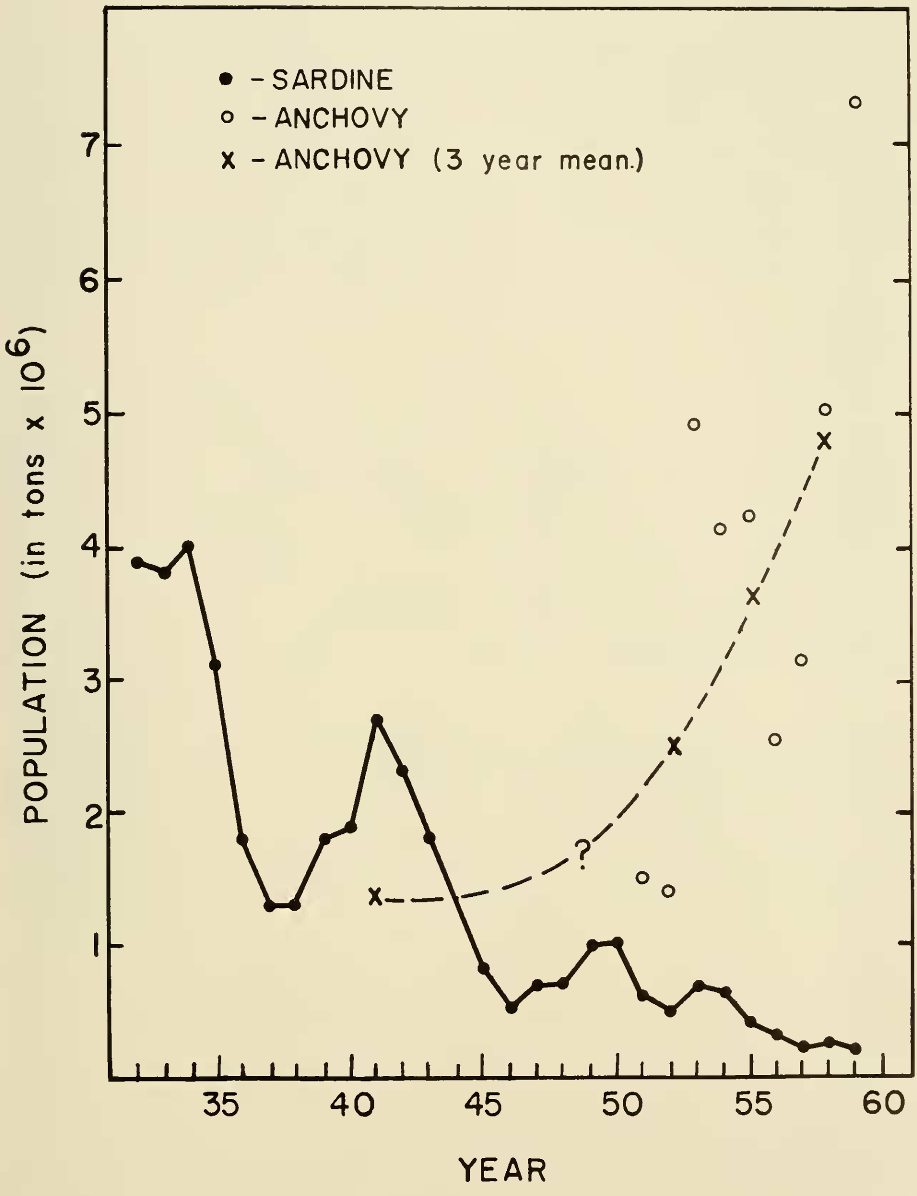

Figure 17. History of sardine and anchovy populations. Sardine estimates from table 15. The 1941 anchovy estimate from text, page 62. The 1951 to 1959 estimates of anchovies derived by multiplying the ratio times the estimated biomass of sardines (table 19). Dotted line drawn between pooled 3-year means as the individual estimates are based on ratios and are exceedingly sensitive to sampling errors.

mechanism(s) involved in the interaction, these observations can be made compatible with the competition hypothesis if it is advanced that the decline of the sardine population, which was induced by the fishery, took place at a greater rate than the anchovy population could grow. In 1932 there was an enormous sardine population and, presumably, a small anchovy population. We can assume that the combined populations were stressing their environment to an extent compatible with the well-being of the individuals, and that the relative balance between them was a function of the overlap between their niches and the relative magnitudes of their innate capacities to increase $\left(\frac{1}{P}\frac{dP}{dt}\right)$.

Now, reduce the sardine population rapidly by fishing. Short life cycle invertebrates might temporarily utilize the released food, *i.e.*, the fugitive species concept of Hutchinson (1951), but the anchovy population would be expected to increase and eventually utilize the resource made available by the decline of the sardine population. One interesting observation to this point is that until the late 1950's the anchovy seemed confined to a few miles offshore, and certainly its spawning was centered there. Now, *e.g.*, 1960, it spawns far offshore (up to 200 miles) in a pattern similar to that formerly characteristic of the sardine.

In the context of the Ricker model, the parameter P_r for the anchovy population has been increased. In the case of the sardine, the parameter P_r, which is a function of both the biology of the animal and its living space including its competition, cannot be as large now that the anchovy population has grown. This being the case, the present (1960) sardine population, even if relieved of fishing pressure, would grow at a smaller rate than that predicted by the population parameters prevailing during the 1932–1948 period before the anchovy population became so large.

The problem of two competing species in the context of a resource (food) in short supply has received formal treatment most recently by Larkin (1963). The basic framework employed is analogous but not homologous to the sardine–anchovy situation, just described, in that the equations do not allow for time lags such as we have observed. Nevertheless, the theoretical analysis predicts the same sort of result that has been observed, supporting the qualitative arguments, and can afford guidance with respect to the outcome of attempts to alter the present "equilibrium" of the sardine and anchovy, *e.g.*, reverse the dominance.

Larkin used a computer to simulate two "competing" species and a selective fishery. He used the classical competition model of Lotka-Volterra, the equations for which are, in Larkin's notation:

$$\frac{dN_1}{dt} = r_1 N_1 - a_1 N_1^2 - b_1 N_1 N_2,$$
$$\frac{dN_2}{dt} = r_2 N_2 - a_2 N_2^2 - b_2 N_1 N_2.$$

The parameters are r, the intrinsic rate of natural increase which would be approached if no limitations were placed on the increase in numbers of the respective populations if they were living alone; a, the compensatory or intraspecific reaction term; and b, the effect of each species on its competitor. All of the parameters are assumed to be positive (or zero).

In the case of a multiple spawner, a fishery affects the model by reducing r, *i.e.*, by an amount related to the difference between potential reproduction and actual reproduction, and, of course, by reducing N. The conclusions of Larkin's study confirm those of other workers, *e.g.*, Slobodkin (1962) and D'Ancona (1954). Most pertinent to the problem at hand is the finding that any exploitation schedule applied to one species in the presence of competing species will produce results differing from those in a single species system; *e.g.*, the equilibrium level of the exploited species will always be lower than if there were no competition. Not enough is known of the sardine–anchovy system to evaluate the equations precisely, but the results obtained by Larkin describe, in a general way, the history of the observed system, and suggest it can be reversed.

It is worth noting that for populations in steady state, the interaction constants must always be smaller than r. The maximum possible value of b_1 is r_1/N_2 and of b_2, r_2/N_1. Therefore, if both populations are large, the constants will be very small and low-level interaction can determine the outcome. The possibility of observing this directly seems remote. Rather, the research strategy must involve qualitative identification of interactions, followed by observation of the integrated results of natural events or experimental field treatments, *e.g.*, altering harvest rates, that should affect them. These can be supplemented by the observation of relatively very small laboratory populations.

SOME PRACTICAL CONSIDERATIONS

A study such as this can guide society towards the most prudent way to treat a resource if the natural system is sufficiently well understood to permit predictions. Therefore, an attempt will be made to explore the problems of obtaining a sustained harvest.

Initially, we can consider the two sardine populations, *i.e.*, 1932–1948 and 1949–1957, without relation to each other or to possible interactions with anchovies. The maximum sustained yield from each population can be estimated from the Ricker functions which were evaluated without introducing

adult density dependent natural mortality and growth. It occurs at the population size where the reproduction curve has its maximum divergence from the $R/P = 1.0$ line, *i.e.*, where some line with a slope of +1 is tangent to the Ricker line. This population size can be located graphically, or by solving the following equation by iterative means:

$$e^{(P_r - P)/P_m}\left(1 - \frac{P}{P_m}\right) = 1. \tag{20}$$

In many situations, P for maximum sustained yield can be satisfactorily estimated by $P = -2P_m + 4P_m^2 + 2P_m P_r$. If the species spawns only once, the maximum sustained yield is simply the difference between P and R at the indicated population size. In a multiple spawning species, the computation is more complex because an individual's potential for replacement can be spread over several years if it is not caught.

The procedure adopted was as follows. The values of R, or potential reproduction for maximum sustained yield, were obtained from the Ricker equations (figs. 9 and 10). These curves were based on a mortality schedule and growth schedule that did not involve fishing mortality. The imposition of fishing mortality too will reduce R below the value of potential reproduction. The approach, then, was to find by iteration a total mortality schedule that would exactly reduce to the equilibrium value the potential reproduction predicted by the Ricker function, *i.e.*, when $R/P = 1$. The difference between the derived Z's and the natural mortality coefficient is the fishing mortality coefficient, and from this the maximum sustained harvest can readily be calculated. It is, as expected, always less than the difference between the spawning stock biomass (P) and the potential reproductive biomass (R). Two other minor computational complexities are involved. The fishing mortality of 2-year-old fish was computed as 0.557 times the rate for older fish for the period 1932–1948, and 0.290 for the later period (tables 11 and 12). The second adjustment was made to overcome the fact that the predicted potential reproduction from the Ricker model is, in a sense, a geometric mean because of the procedure used in estimating the parameters of the function. While it represents the most probable value of R at each level of P, it will be less than the arithmetic value (Ricker, 1958a). The latter is the value pertinent to the fishery. Therefore, correction factors based on Jones' (1956) equation for the relation between the arithmetic and geometric mean, easily computed from the variance of the common logarithms of the potential R's, were applied to the estimated maximum sustained yield. The correction is 1.22 times for the earlier period and 1.11 times for the later one.

For the earlier period, the estimated population for a maximum sustained yield was 975,000 tons, and the yield was 470,600 tons annually. During

the 1937–1945 period when the population was near that expected to yield the maximum catch, *i.e.*, 1,000,000 tons, the actual average annual harvest was 570,240 tons. This suggests that the population was "overharvested" by about 20 per cent. Thus, it seems clear that the population was overfished in an economic sense, and overfished in a biological sense, too, in that the heavy mortality induced by the fishery removed the "cushion" against poor spawning success provided by the older fish.

For the later period, that involving the 1949 and subsequent year classes, a maximum sustained yield of about 57,000 tons would have been provided by a population of about 178,000 tons. The average harvest during the 1954–1958 period was 73,000 tons. Again, there is a clear indication of overfishing, reinforced by the apparent continuing decline of the population. By 1959, the population had declined to 190,000 tons from 668,000 tons in 1954, and the more recent record suggests it is now (1963–1964) close to 100,000 tons. Two factors must be considered in interpreting the 1949–1957 results. First, the basis of the computed population parameters for this period involves some uncertainties as to detail, particularly in 1949–1950, and the estimates are based on very few years.

The problem of the reality of a maximum sustained yield in a fluctuating environment was first considered by Ricker (1958b) and later reexamined by Larkin and Ricker (1964). For populations fitting the Ricker function described above, they found that if the rate of exploitation is held constant at that which is predicted to give the maximum sustained yield, the average catch over a period of years will approximate the expected catch, despite randomly generated variation larger than that observed for the sardine. The yield, of course, fluctuates widely from year to year. They also found that the yield could be increased beyond the predicted by allowing just the requisite spawning each year. This would involve no fishing in some years and extra fishing in others. Their studies were based on single spawners. A multiple spawning population introduces complexities in detail but not in principle. The possibility that good and bad years are not random events (discussed earlier) in the sardine environment adds another complication.

Ricker and Larkin did not consider an unregulated fishery such as that for the sardine. If fishing pressure is too intense, the population size will not oscillate around the one giving the maximum sustained yield, but will fall to some lower level. If the lower population level is accompanied by a contraction of range that maintains the relative accessibility of the population, fishing mortality rates will tend to increase or remain stable and the population will be forced to an even lower level during the next sequence of poor spawn survival. This seems to be essentially what took place in the 1932–1948 period, and, in view of the exceedingly high fishing rates in 1958–1960 (table 12), may be what is taking place today.

TABLE 20. *Age structure of the spawning population at two different levels of fishing. Half of the 2-year-old fish are considered to spawn.*

1,400,000 Tons $F_2 = 0.28$; $F_{3-10} = 0.50$; $M = 0.40$				975,000 Tons $F_2 = 0.43$; $F_{3-8} = 0.78$; $M = 0.40$			
Age	*Relative Number*	*Relative Spawning Biomass*	*Cumulative Spawning Biomass*	*Age*	*Relative Number*	*Relative Spawning Biomass*	*Cumulative Spawning Biomass*
2	1,000	282	282	2	1,000	357	357
3	507	378	660	3	434	409	766
4	206	190	850	4	133	155	921
5	84	86	936	5	41	53	974
6	34	38	974	6	13	18	992
7	14	16	990	7	4	6	998
8	6	7	967	8	1	2	1,000
9	2	2	999				
10	1	1	1,000				

Can this be avoided? Presumably, if it had been possible during the 1932–1948 period to hold the fishing mortality rate at the optimum level calculated from the Ricker function, the population would have oscillated around 975,000 tons, even in the face of nonrandom environmental variation. Had the catch been regulated in accordance with spawning success, even higher yields might have been obtained, judging by Larkin and Ricker's (1964) results. It is, however, not entirely clear how the harvests appropriate to spawning success could have been determined because it has not been possible to estimate recruitment until the third year, and, therefore, regulatory changes would always be well behind the events they sought to compensate.

An alternative approach would be to maintain the population at a higher level which, because of the age structure (table 20), would supply a buffer against environmental variability. For example, if the population were maintained at 1,400,000 tons, the steady state yield would be 383,000 tons per year, or 81.4 per cent of the maximum. This harvest could be achieved with only two-thirds the effort ($F = 0.50$ instead of 0.75) for 3-year and older fish. Four consecutive disasters, defining a disaster as a year in which spawning success is 50 per cent of expected, would reduce the population to about 812,000 tons, but it would still be large enough to grow at almost its absolute maximum amount per year ($P_m = 975{,}000$ tons). Until such a time as good or poor year classes can be predicted or measured well in advance of their joining the spawning and harvested population, and the harvest appropriately adjusted, the sardine fishery will have to accept either undesirably wide fluctuations in yield or smaller but more stable yield.

As already indicated in the discussion of the anchovy, it may be completely unrealistic to count on a large sustained sardine harvest of the sardine in

the California Current system because of competition from other species. The exploratory studies of Larkin (1963) offer some practical guidance, for they show that appropriate harvest schedules applied to both species can result in maintaining both in large numbers, while maximizing the combined yield. It might be argued that some third species would then emerge as significant, but it seems likely that this third species would be similar in habits to the sardine and anchovy, and, thus, also harvestable. If this process were carried to the limit, however, the ocean might ultimately be populated by organisms with very short life cycles. In general, these are small, and of little use to man at the present time. Thus, the intelligent use of living resources by man must be based on a thorough understanding of the total ecology of the communities involved, and it is unlikely that this would be dominated by any single environmental factor.

The question of whether the observed decline of the sardine could have happened naturally in an unfished population also has practical and ecological significance. The sardine is, in a sense, imperfectly adjusted to its environment, as demonstrated by the record of spawning success (fig. 9), which shows violent fluctuations with about half the year classes only half as large as predicted by the Ricker model, and, more to the point, well below the equilibrium line. If the probability of a year class being below the equilibrium line is 0.5, on the basis of random expectation, ten such events in sequence will have an expectation of occurrence of one every 2,048 years, on the basis of probability theory. Such a sequence, presumably a response to density independent factors in the ocean environment, would drastically reduce even a relatively long-lived unfished sardine population. Such a decline could then occur naturally over a reasonably short time span. Would it have occurred during this period? This can never be answered with certainty for obvious reasons. However, the 1932–1948 reproduction record (fig. 9) suggests the population could have been maintained at the level of maximum yield had fishing pressure been adjusted appropriately. The 1949–1957 record (fig. 10) cannot be brought to bear because the population was qualitatively different from the previous period. Finally, though the density independent variations in reproductive success are almost certainly a function of the environment, it has not yet been learned what environmental factors are important. Temperature, for example, is not related in any obvious way to reproductive success. Perhaps more to the point, the population has declined fairly steadily since 1932. The natural environment has varied widely. The only constant factor has been steady fishing pressure. Perhaps the only completely defensible conclusion is that a species with a large environment-induced element in its reproductive dynamics can be more easily overfished than one whose reproductive success is closely governed by density dependent processes.

The anchovy, on the other hand, might be considered better adjusted to

the changing environment than the sardine. It is a much shorter-lived species; in the virtually unfished stock, individuals over 4 years of age are rare and 7 years seems to be the greatest age (Miller, 1956). With so few ages comprising the population, the species must be less tolerant of wide fluctuations in spawning success, *i.e.,* be more closely controlled by density dependent processes. The relatively steady rise of the anchovy population (table 19) in the face of much environmental variation suggests that this is so. This relative stability, *i.e.,* never spectacularly good nor spectacularly poor year classes, may also have been a factor in the relatively slow replacement of the sardine by the anchovy.

Given these properties of the two species even in the absence of a fishery, a series of poor years for the sardine might allow the anchovy to preempt much of the energy supply in the environment and in so reducing the environment for the sardine, reduce the size of its maximum equilibrium level (P_r). Once the sardine population was seriously reduced, it would take a series of very good years for the sardine to reestablish itself as the dominant form.

If these speculations are correct, the anchovy might provide the basis for a more stable yield than the sardine. It also seems quite likely that reducing the anchovy population somewhat by fishing would result in a resurgence of the sardine, providing the fishing for the sardine was reduced to a level that would permit the population to grow.

DISCUSSION OF OTHER STUDIES

As already indicated, there have been several recent attempts to explore the population biology of the Pacific sardine and to ascertain the causes of the decline, or at least apportion the relative effect of the fishery and events in nature. All of these studies, including the present, agree on the obvious; that is, removals were greater than replacements. All of the previous studies are based on virtual population estimates, accounting for many of the differences between their conclusions and those of the present study.

Radovich (1962) assumed a parabolic relation between stock size and year class size. This involves an assumption of zero reproduction at zero stock size which is realistic, and zero reproduction at some larger stock size which is not realistic. In addition, symmetry is assumed, which, especially since year class size instead of rate of population growth is under consideration, remains unevaluated. Further, he used the virtual population and numbers of fish (instead of biomass), both of which induce serious underestimation of the population during the early years when fishing effort was low and the population was comprised of older fish.

Despite the lack of a theoretical basis of the model used by Radovich and use of the virtual population uncorrected for biomass, at least one important conclusion is compatible with this study. That is, maximum reproduction

is obtained at the stock size prevailing during the 1937–1939 period, a conclusion also reached by Clark in Clark and Marr (1955) by simply inspecting the data.

Another conclusion of Radovich at variance with this study concerns genetic races. Two have been identified, and a severe reduction of one (the northern) was associated in this study with the change in the population associated with the recruitment of the 1949 year class. Though he had no direct evidence, Radovich proposed that the collapse of the Oregon–Washington–British Columbia fishery after 1948 was associated with the collapse of yet a third race. It is impossible to fully refute such an argument. One can only observe that the tag returns have not been analyzed in a way that supports the assertion of a third stock. Finally, it is not necessary to invoke a third race to explain the collapse of the northern fishery. Based on population size and age composition in 1949 and 1950, as compared to its size and age composition during earlier years, together with the age composition of the Pacific Northwest catches, the maximum expected catch during 1949 and 1950 would have been no larger than 2,000 tons, hardly enough to activate an industry geared to over 50,000 tons. Thus, the observed quantitative changes in the population offer a sufficient explanation of events without introducing the undocumented qualitative change in the population proposed by Radovich (1962).

Marr (1960, 1963) has also considered the dynamics of the sardine population. The portions of his 1960 paper under consideration here have been expressed in his 1963 paper. Marr is in general agreement with this study with respect to the course of events, *i.e.,* decline of the northern race first, but he holds that ". . . this series of small year-classes resulted from an unfavorable oceanographic regime, rather than a reduction in the size of the spawning population." He further holds that ". . . the unfavorable environment (reduced temperatures) is mediated through competition with the northern anchovy." More specifically, he holds that a year (before the onset of spawning) that is cool disadvantages the sardine by presumably delaying its spawning relative to the anchovy which spawns at about 2° C. lower temperatures, thus placing the sardine larvae at a competitive disadvantage.

This is not necessarily so. Presumably the anchovy will always tend to spawn first whatever the temperature regime, *i.e.,* warmer or cooler than average. In fact, in the absence of evidence it could be argued that the difference in spawning temperature reduces competition between the species. The hypothesis is also open to question from scaler considerations. Marr's annual temperature index (which reflects the entire year) only varies by plus or minus 5 per cent. His year classes vary over three orders of magnitude. It seems more logical, *a priori,* to expect a species to evolve mechanisms

that filter out the effect of environmental variations rather than amplify them. Even during the coldest year of his series there were only 2 months (January and February) when temperatures were below the threshold of the sardine. Finally, there is the empirical evidence that 3 very warm years in series (1957, 1958, and 1959) resulted in year classes of the same order, relative to stock size, as the preceding cold years. Thus, the long series of poor year classes (1949–1963) at small stock sizes in the face of a varying oceanic climate suggests that Marr's conclusion that year class size is independent of stock size is untenable.

There is no question that the environment has induced large variations in spawning success. There is also no question that the one environmental factor that has remained constant throughout the decline has been continued heavy fishing pressure. There is also no question that the anchovy has risen to replace the sardine in the ecosystem. This fact alone strongly suggests that the niches of the two species overlap a great deal. In this respect the suggestions of Marr and other workers that the two species interact is realistic. It is also realistic to conclude that the development of a large anchovy population has altered the environmental framework of the sardine so that the dynamics of that population are now different from those prevailing prior to 1955. It is interesting to note that man can easily alter both of these "environmental parameters," *i.e.*, fishing pressure on the sardine and the size of the anchovy population, and thus experimentally test these hypotheses.

The final major recent study is that of MacGregor (1964). He used the virtual population as a basis for study. It is pertinent to comment on two aspects of his study here. One, explicitly considered by MacGregor, is his finding of significant negative correlations between stock size and year class size. The other is the existence of cycles, discussed by MacGregor.

None of the correlations presented by MacGregor are significant when the population estimates developed in this study are used. The difference, of course, must rest in the basis of the two series of population estimates. This can be readily demonstrated by considering the two negative correlations involving 1932 and subsequent years (MacGregor, table 3). Fishing effort (and mortality) was increasing from 1932 to 1936 (table 11, this paper), causing the virtual technique to grossly underestimate the spawning population (relative to later years) and to a lesser extent the 1932 and 1933 year classes. This, for example, leads to associating a large 1932 year class with a small 1932 spawning stock, whereas the estimates developed in this study relate a large spawning stock to a large year class. MacGregor's third significant negative correlation ($p = 0.01$) involves the years 1945–1950. A suggestion of negative correlation is also evident in the estimates of this paper (figs. 9 and 10), but a positive association exists over the years 1941–1946. The principal source of difference between MacGregor's 1945–1950

series and mine lies in the 1949 and 1950 year classes which were quite unavailable to the fishery during their second and third years of life and thus grossly underestimated by the virtual technique.

MacGregor, accepting his negative correlations of stock size and year class size, concludes that stock size is determining year class size during all years except the few that separate his sets of negative correlations. He apparently assumes that these transition years are periods during which qualitative changes in the population occurred. The results of this study do not support these conclusions. The only qualitative change in the population that was identified is that associated with the recruitment of the 1949 year class, and, as already indicated, MacGregor's sets of negative correlations cannot be generated from the population estimates of this study. Apart from the general relations of stock size and year class size depicted by the computed Ricker lines (figs. 9 and 10), the variation in year class size is more probably ascribable to the environment.

MacGregor suggests his negative correlations and the attendant suggestion of cycles (see figures 3 and 11) may be an example of the self-generated cycles described by Ricker (1954). This seems untenable from the results of this study. Nevertheless, there is a hint of cyclic variation in year class size (fig. 8). The major periods are 4, 10, 5, and 5 years in length (trough-to-trough starting with 1930). These periods are neither regular nor do they correspond well with twice the mean age of the spawning stock, *e.g.*, 4 years in 1932 and 3.6 years in 1950. Although it cannot be shown how, nor can the regime(s) be identified, it seems more likely that these "cyclic" perturbations in year class strength that are independent of spawning stock size are associated with trends in the ocean environment. The ocean environment fluctuates, and the deviations persist for periods similar to the length of the cycles noted above. For example, 1948 to 1956 (9 years) were persistently cool off California and 1957–1959 (3 years) were abnormally warm. (However, temperature changes, at least the simple published indices, have not been linked with the changes in spawning success in any meaningful way.)

SUMMARY AND CONCLUSIONS

1. The catch of the Pacific sardine rose from 28,000 tons in 1916 to nearly 800,000 tons in 1936. This growth can be attributed to an increasingly intensive fishery. After a period of relative stability which ended in 1945, the landings diminished until today (1964) they are on the order of 20,000 tons. The decline in landings was largely a function of a shrinking population.

2. In order to extract estimates of population size from the catches and other data, a new method of solving the catch equation was devised. This method overcomes the effect of the varying availability of the population to the fishery from year to year, a difficulty that had heretofore hindered critical

examination of the population. The method also provides a framework to which all of the available information on population size can be related. The formal solution requires, in addition to aged landings, only two additional sources of information, *e.g.*, two independent estimates of the fishing mortality coefficient for any set of years. The advantages of applying this method are that it removes the effect of several biases from the data, and perhaps most important provides estimates of absolute, as opposed to relative, abundance.

3. The method was applied to the sardine catch statistics for the years 1932 to 1960. In the course of analyzing these statistics, together with consideration of all other available information, it became evident that the parameters of the population changed appreciably beginning with the recruitment of the 1949 year class to the spawning population. The qualitative change associated with the change in parameters was the reversed dominance of the two races comprising the population. Previous to the recruitment of the 1949 year class the northern race dominated; afterwards the southern race dominated.

4. For the earlier period (1932–1948), the two extra degrees of freedom used in computation were a value for the natural mortality coefficient of 0.40, and a value of the fishing mortality coefficient for 1950 of 0.79. The natural mortality value was derived from several analytical considerations. The fishing mortality was derived by a survey-catch analysis.

5. For the later period (1949–1960) the extra information was derived from egg-survey estimates of the population for the years 1954 to 1958, and from the trend evidenced by these surveys. A natural mortality coefficient of 0.80 was the best estimate.

6. The solutions of population size (numerical and biomass), and the attendant fishing and natural mortality coefficients were shown to be consonant with all other information on the population, *e.g.*, the results of tagging experiments. The population was almost 4 million tons in 1932 and less than 200,000 tons in 1959.

7. The relation between spawning stock size and reproductive efficiency was examined using the Ricker function. The equilibrium value of the population was estimated at 2.4×10^6 tons. This analysis showed that it is improbable that the population would have declined in the absence of fishing, whereas the fishing rates applied to the population lowered reproduction to an extent that a decline was inevitable.

8. The qualitative change in the population attending the recruitment of the 1949 year class was associated with a markedly reduced population comprised of few age-classes. There was a "reproductive failure" of the northern race during 1949 and, possibly, 1950. This race, lacking the resilience supplied by older fish, then collapsed.

9. The sardine population at 1932 levels was an important, if not the

dominant, consumer of energy in the California Current system. Its collapse was followed by a marked increase in the northern anchovy so that now (1957–1959) it appears to have replaced the sardine. Its population is estimated at 4.8 million tons (the sardine was about 4.0 in 1932), and as its energy requirements are the same, its role in the energy budget must be similar.

10. The maximum sustainable yield of the pre-1949 population was 471,000 tons at a spawning population size of about one million tons. During this period the catch averaged 570,000 tons. In addition, the heavy fishing left too few older individuals to "cushion" the population against reproductive failures.

11. Apart from the general relation between population size and year class size, there is variation in spawning success that cannot be associated with spawning-stock size. This is in the order of 7 × at a given stock size. This variation is nearly as large as that that can be associated with population size. The latter is about 9 ×, associated with an 18 × range in population size (1932–1957).

12. The maximum sustainable yield for the present population is 57,000 tons at a population of 178,000 tons. The present population was also overfished, and apparently continues to be.

13. The rise of the anchovy was apparently in response to the environmental void created by the decline of the sardine. If this is so, the validity of a sustainable yield of sardines can be questioned, for the reduced sardine population required to generate the yield would also release resources to the anchovy. The subsequent increase of the anchovy would surely alter the parameters of the sardine population in such a way as to reduce the maximum sustainable yield. As a converse, the present situation is not likely to alter rapidly, even if sardine fishing is stopped, unless man or nature acts to reduce the anchovy population somewhat. It appears that judicious utilization of all ecologically similar species within a trophic level offers the only hope for sustained yields.

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APPENDIX 1.

Estimation of Age Distribution of 1938 Catch

Materials for age determination, *i.e.,* scales or otoliths, were not taken during 1938. Length frequency and weight data were taken. From these and the total tonnage the total numbers in the catch have been estimated. Wolf (1961) attempted to estimate the age composition from a modal analysis of the length frequency distribution. His results in millions together with the age distribution of the adjacent years are as follows:

Year	0	1	2	3	4	5	6	7+
1937	3	104	639	278	315	206	54	37
1938	7	1,433	1,155	140	93	61	127	34
1939	–	386	1,248	734	167	35	45	14

These data when transformed to catch per boat month in thousands are as follows:

Year	0	1	2	3	4	5	6	7+
1937	3	129	797	346	393	256	68	43
1938	8	1,544	1,245	151	100	66	137	95
1939	–	461	1,491	877	199	42	54	15

Though Wolf's procedures were objective, the results are not completely satisfying. The most prominent difficulty is that his age structure in 1938 is not compatible with that of the adjacent years. Another problem is that his catch of 1-year-olds is twice as high as any other year on record. These observations lead me to conclude that his method resulted in misclassification.

Accordingly an alternate procedure that is based on the assumption that the classifications during 1937 and 1939 are correct was devised. First, a catch per unit of effort base was established by computing S^* for the 1937–1939 interval; the square root of this value (0.322) provides an estimate of the 1937–1938 and 1938–1939 intervals. Using this value, the estimated numbers of fish 4 years and older for 1938 was computed from the 1937 data on fish 3 years and older. Similarly, the numbers of 4-year-olds in 1939 yielded an estimate of the 3-year-olds in 1938. The thusly derived sum of the 3-year-old and older fish is 64 per cent larger than Wolf's total. This amount was substracted from his total of 1-year-olds, on the aforementioned grounds that his figure was almost certainly too high. Since there is no basis

for reexamining Wolf's estimate of the incompletely recruited 2-year-olds, his value was retained. It is worth noting that his value is consistent with the strength of that year class in subsequent years.

In interpreting the results of this procedure, *i.e.,* r values and population values for 1938, it is clear that the r value is an artifact. The population of 3-year-olds and older is correct if the assumption that the border values (1937 and 1939) provided a valid estimate of the true relative age composition in 1938, because the abundance estimate is controlled by their measured abundance in 1937 and 1939. The estimate of the 2-year-olds is dependent on the validity of Wolf's estimate. The 1-year-olds do not enter the analyses.

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